Z.
072Aa
O
B

BRITISH MUSEUM
NAT. HIST.
4 FEB 1977
PRESENTED
ZOOLOGY LIBRARY

BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY)

ZOOLOGY

Vol. 22

1971–1973

BRITISH MUSEUM (NATURAL HISTORY)
LONDON: 1977

DATES OF PUBLICATION OF THE PARTS

No. 1	5 October 1971
No. 2	31 December 1971
No. 3	31 December 1971
No. 4	3 March 1972
No. 5	3 March 1972
No. 6	29 March 1972
No. 7	30 March 1972
No. 8	14 June 1972
No. 9	16 March 1973

ISSN 0007–1498

Printed in Great Britain by John Wright and Sons Ltd. at The Stonebridge Press, Bristol BS4 5NU

NAT. HIST. LIBRARY

CONTENTS

ZOOLOGY VOLUME 22

		PAGE
No. 1.	Hyoid and ventral gill arch musculature in osteoglossomorph fishes. By P. H. GREENWOOD (Pls 1–2)	1
No. 2.	The clupeoid fishes described by Francis Day. By P. K. TALWAR & P. J. P. WHITEHEAD	57
No. 3.	Fine structure of *Bodo saltans* and *Bodo caudatus* (Zoomastigophora: Protozoa) and their affinities with the Trypanosomatidae. By B. E. BROOKER (Pls 1–6)	87
No. 4.	The type specimens and identity of the species described in the genus *Lithobius* by C. L. Koch and L. Koch from 1841 to 1878. By E. H. EASON	103
No. 5.	Contributions to the life-histories and development of *Cucullanus minutus* Rudolphi, 1819 and *C. heterochrous* Rudolphi, 1802. By D. I. GIBSON	151
No. 6.	Bats from Thailand and Cambodia. By J. E. HILL & K. THONGLONGYA.	171
No. 7.	A redescription of *Spelaeomysis servatus* (Fage) comb. nov. (Mysidacea Lepidomysidae) from the material collected on Aldabra Atoll, with a key to the species of Lepidomysidae. By R. W. INGLE	197
No. 8.	Recent records of mammals (other than bats) from Ethiopia. By G. B. CORBET & D. W. YALDEN	211
No. 9.	The shell structure and mineralogy of the Bivalvia. II. Lucinacea–Clavagellacea conclusions. By J. D. TAYLOR, W. J. KENNEDY & A. HALL (Pls 1–15)	253
	Index to Vol. 22	295

HYOID AND VENTRAL GILL ARCH MUSCULATURE IN OSTEOGLOSSOMORPH FISHES

P. H. GREENWOOD

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 22 No. 1
LONDON : 1971

HYOID AND VENTRAL GILL ARCH MUSCULATURE IN OSTEOGLOSSOMORPH FISHES

BY
PETER HUMPHRY GREENWOOD

Pp. 1–55; 21 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 22 No. 1
LONDON : 1971

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series, corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 22 *No.* 1 *of the Zoological series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation
Bull. Br. Mus. nat. Hist. (Zool.).

© Trustees of the British Museum (Natural History), 1971

TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 5 *October*, 1971 *Price* £1·80

HYOID AND VENTRAL GILL ARCH MUSCULATURE IN OSTEOGLOSSOMORPH FISHES

By P. H. GREENWOOD

CONTENTS

		Page
INTRODUCTION		4
MATERIALS AND METHODS		7
HIODONTIDAE:	*Hiodon alosoides*	9
OSTEOGLOSSIDAE:	*Osteoglossum bicirrhosum*	12
	Scleropages leichardti	13
	Heterotis niloticus	14
	Arapaima gigas	14
PANTODONTIDAE:	*Pantodon buchholzi*	16
NOTOPTERIDAE:	*Papyrocranus afer*	18
	Xenomystus nigri	21
	Papyrocranus and *Xenomystus* compared with *Notopterus*	22
MORMYRIDAE:	*Mormyrus kannume*	23
	Mormyrus caschive	27
	Mormyrus lacerda	28
	Mormyrus hasselquisti	28
	Cyphomyrus discorhynchus	30
	Marcusenius cyprinoides	31
	Marcusenius victoriae	32
	Gnathonemus longibarbis	32
	Campylomormyrus elephas	33
	Petrocephalus bane	35
	Petrocephalus catostoma	37
	Isichthys henryi	37
	Mormyrops anguilloides	38
	Hyperopisus bebe	40
GYMNARCHIDAE:	*Gymnarchus niloticus*	44
SUMMARY AND DISCUSSION		48
	Phyletic relations within the Superorder	53
ACKNOWLEDGEMENTS		54
REFERENCES		54

ABSTRACT

THE ventral hyoid and gill arch musculature in several representatives of all osteoglossomorph families is described and compared. The results of this survey show clearly the unusual specializations of the Mormyridae, and add evidence to the

suggested relationships of the Mormyridae to the Notopteridae. The Osteoglossidae and Pantodontidae show a different (and more usual) type of specialization. The Hiodontidae have a basic teleostean pattern in the hyoid muscles, not far removed from the *Amia* pattern.

Based on these and other characters, a new intragroup classification is suggested for the Osteoglossomorpha (including the reduction of the Gymnarchidae to subfamilial status within the Mormyridae).

INTRODUCTION

Although the ventral gill arch and hyoid musculature has been described (with varying degrees of thoroughness) for some osteoglossomorph fishes (Holmquist, 1911; Munshi, 1960; Bishai, 1967; Nelson, 1969), to date there has been no fully comparative account of these muscles; furthermore, only a few species have been investigated.

The present study is an attempt to fill both these gaps, and is part of a continuing investigation of intragroup relationships among the Osteoglossomorpha. That the musculature might provide some information on this subject is suggested by Nelson's (1969) examination of dorsal and ventral gill arch muscles in certain notopterid, mormyrid, osteoglossid and hiodontid species. Nelson's results are somewhat equivocal (and some are modified by my study), but if the hyoid musculature is also taken into account, a rather different picture emerges.

Nomenclature. For the gill arch muscles I have followed the nomenclature used by Nelson (1967 and 1969) which, in turn, was based on the terminology of Vetter (1878) and Edgeworth (1935).

The hyoid muscles provide something of a nomenclatural problem. The major muscle connecting the hyoid bar with the lower jaw is generally called either protractor hyoideus or geniohyoideus. (See Holmquist, 1911; Dietz, 1912, Edgeworth, 1928 and 1935; Munshi, 1960, and Osse, 1969 for discussions of this problem). It is clear that on grounds of homology and ontogeny (Edgeworth, *op. cit.*) the muscle should not be called a geniohyoideus in teleost fishes.

Associated with this muscle there is usually a much smaller, transverse muscle, the so-called intermandibularis, which lies anteriorly between the rami of the jaws.

As Holmquist (*op. cit.*) suggested, and Edgeworth (1928) later demonstrated embryologically, the protractor hyoideus is a compound muscle derived from an intermandibularis component anteriorly (the so-called posterior intermandibularis as distinct from the transverse anterior intermandibularis), and an interhyoideus component posteriorly.

Among the osteoglossomorphs studied, the protractor hyoideus shows, at least superficially, varying degrees of complexity or unity. In many osteoglossoids it appears to be a single muscle, in hiodontids a single muscle obviously of compound origin, and in mormyrids and notopterids a group of distinct muscles. Thus, in osteoglossoids I shall refer to this muscle as the protractor hyoideus, and in the notopterids and mormyrids the components will be named (*viz.* interhyoideus and posterior intermandibularis). The use of the term "protractor" here is purely

nominal and does not imply any functional attributes (see Osse, *op. cit.*). In most species the anterior intermandibularis is clearly identifiable despite its great variation in size and area of attachment.

There is general agreement on the nomenclature for that part of the constrictor hyoideus ventralis associated with the branchiostegal rays, namely the hyohyoideus. and that term is used in this paper.

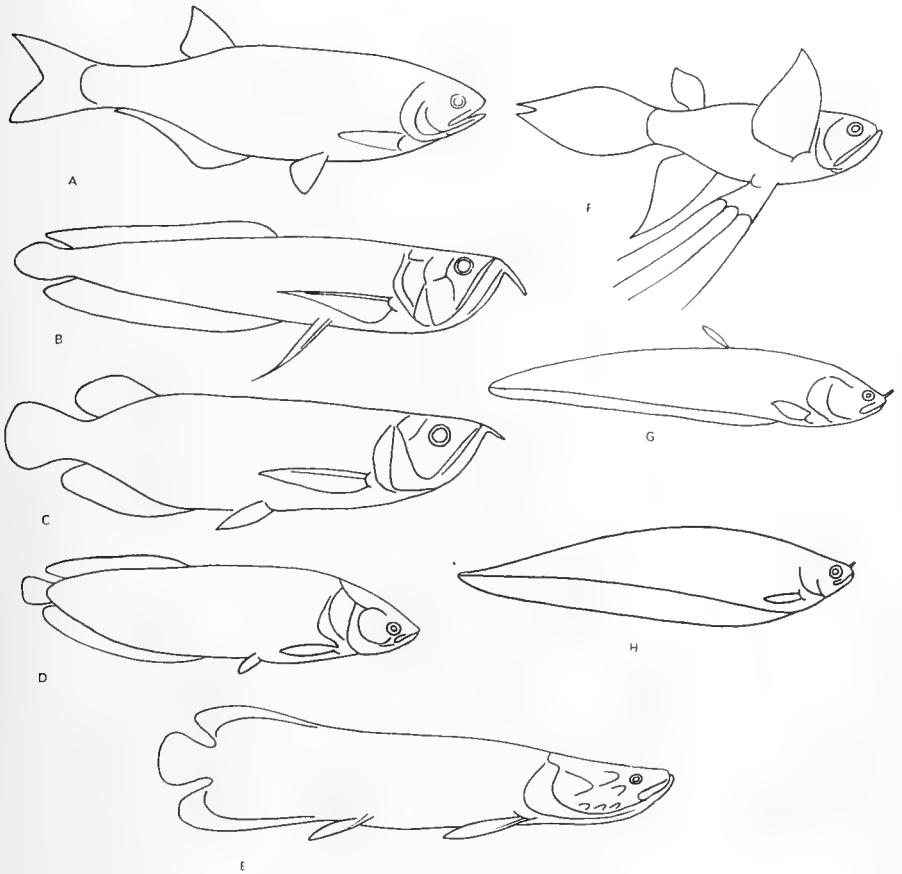


FIG. 1. Outline drawings, not to scale, of: A. *Hiodon alosoides*. B. *Osteoglossum bicirrhosum*. C. *Scleropages leichardti*. D. *Heterotis niloticus*. E. *Arapaima gigas*. F. *Pantodon buchholzi*. G. *Papyrocranus afer*. H. *Xenomystus nigri*.

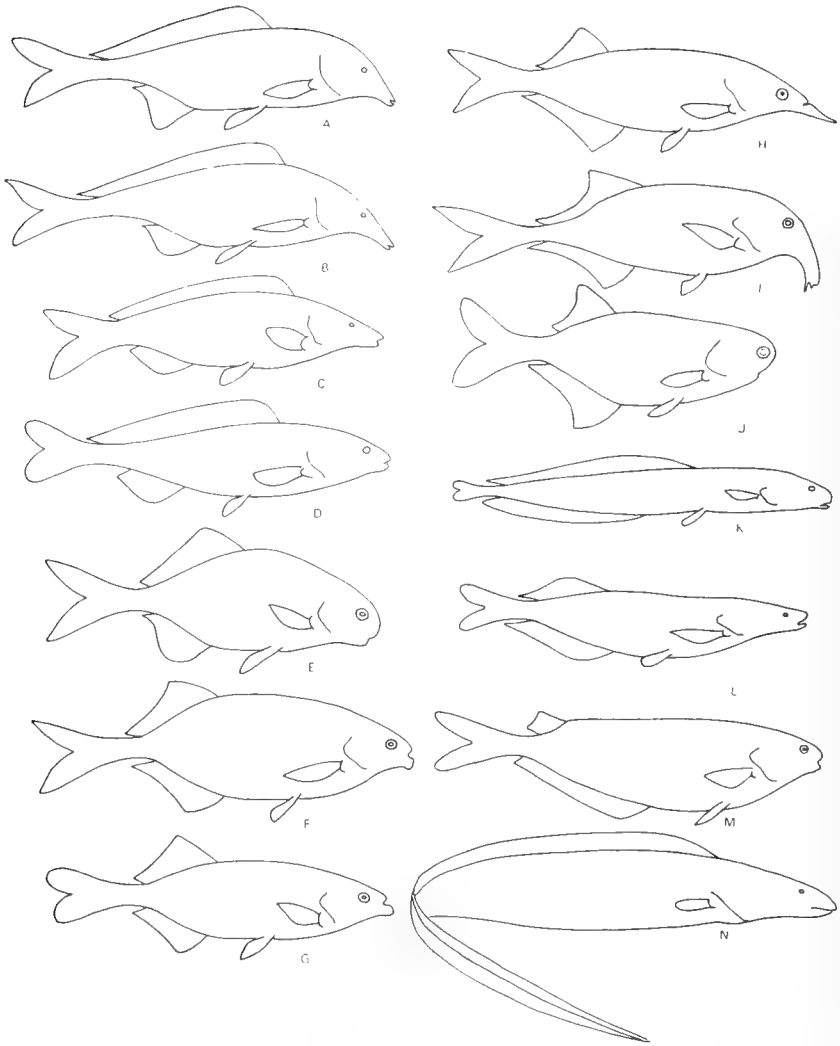


FIG. 2. Outline drawings, not to scale, of various mormyrid species: A. *Mormyrus kannume*. B. *Mormyrus caschive*. C. *Mormyrus lacerda*. D. *Mormyrus hasselquisti*. E. *Cyphomyrus discorhynchus*. F. *Marcusenius cyprinoides*. G. *Marcusenius victoriae*. H. *Gnathonemus longibarbis*. I. *Campylomormyrus elephas*. J. *Petrocephalus bane*. K. *Isichthys henryi*. L. *Mormyrops anguilloides*. M. *Hyperopisus bebe*. N. *Gymnarchus niloticus*.

MATERIALS AND METHODS

Dissections were made on the following specimens; for most species dried skeletons or alizarin transparencies were also available.

Species	B.M.(N.H.) register number	Standard length, mm.
Hiodon alosoides	1965.7.2 : 1–3	185, 150, 136
Hiodon alosoides	1965.11.23 : 1–8	143, 124, 110, 108, 105
Osteoglossum bicirrhosum	1926.10.27 : 1–2	340, 286
Scleropages leichardti	1966.9.23 : 5	200
Scleropages formosus	1966.9.5 : 1	60
Heterotis niloticus	unregistered	300
Arapaima gigas	unregistered	245
Pantodon buchholzi	1913.3.12 : 1	67
Papyrocranus afer	1969.3.26 : 27	196
Papyrocranus afer	unregistered	290, 225
Xenomystus nigri	unregistered	146, 145, 140, 140, 130
Xenomystus nigri	unregistered	140
Xenomystus nigri	unregistered	145
Notopterus kapirat	1931.7.20 : 9–17	174, 167, 155
Notopterus kapirat	1938.2.22 : 11	213
Mormyrus kannume	unregistered	203
Mormyrus lacerda	1965.3.15 : 316–320	260, 210, 200
Mormyrus hasselquisti	unregistered	240
Cyphomyrus discorhynchus	1966.7.29 : 2–4	137, 137, 125
Marcusenius cyprinoides	1961.12.1 : 48–74	150, 132
Marcusenius victoriae	1961.6.13 : 16	130
Marcusenius victoriae	1962.2.6 : 26	152
Gnathonemus longibarbus	1928.5.24 : 2	150
Campylomormyrus elephas	1928.7.30 : 3–4	136, 134
Campylomormyrus elephas	1919.9.10 : 61	154
Petrocephalus bane	1907.12.2 : 231–232	150, 150
Petrocephalus bane	1905.3.15 : 1–2	110, 104
Petrocephalus bane	unregistered	112, 112
Petrocephalus catostoma	1961.6.21 : 7–18	76, 73, 72, 68, 60
Isichthys henryi	1958.9.18 : 5–6	200
Isichthys henryi	unregistered	270, 240
Mormyrops deliciosus	1969.3.26 : 28	235
Mormyrops anguilloides	unregistered	205
Hyperopisus bebe	1948.6.30 : 1–4	190, 145, 140, 140
Hyperopisus bebe	1969.3.25 : 34	195
Gymnarchus niloticus	1969.3.26 : 49	370
Gymnarchus niloticus	1948.6.30 : 21	330
Gymnarchus niloticus	1902.11.10 : 56	290

Species	B.M.(N.H.) register number	Standard length mm.
Gymnarchus niloticus	1953.7.10 : 5	400
Amia calva	unregistered	48 (head only)
Albula vulpes	1949.11.29 : 1–4	177, 157, 152
Elops saurus	1961.8.31 : 45	134

ABBREVIATIONS USED IN TEXT FIGURES

A: Articular
AIM: anterior intermandibularis muscle
Apn: aponeurosis
ASCh: articular surface for ceratohyal on 1st basibranchial (Nelson's [1968] terminology)
AT: anterior transversus muscle
Bb 1–3: basibranchial, 1st–3rd arch
BhTp: basihyal tooth plate
BrR: branchiostegal ray
BrM: branchiostegal membrane
Bt: basihyal, and its tooth plate, with connective tissue cover
CbI–V: ceratobranchial (arches I–V)
CbM: muscle connecting 4th and 5th ceratobranchials
Ch: ceratohyal
Chc: cartilaginous part of ceratohyal
ChUh: muscle between ceratohyal and urohyal
CL: cleithrum
CT: connective tissue surrounding lateral and ventral edges of basihyal and its anterior tooth plate
CTM: connective tissue mass covering posteroventral end of basihyal tooth plate and articulation of the urohyal
D: dentary
Gr: gill rakers
HaBM: hypaxial body musculature
HbI: hypobranchial (arch 1)
HbII: of second arch
Hhy: hyohyoideus muscle
Hhya: anterior portion of hyohyoideus muscle
Hp: hypohyal
Hpic: hypohyal (cut through)
IH: interhyoideus muscle
IHhy: inferior hyohyoideus muscle
Ihyi: interhyoideus muscle, inner (medial) division
Ihyim: interhyoideus muscle, innermost division
Ihyl: interhyoideus muscle, lateral division
Ihyvl: interhyoideus, ventrolateral muscle
IOp: interoperculum
L: ligament from basihyal tooth plate (to urohyal)
LUh: ligament from urohyal to hypohyals
Max: cut end of maxilla
Mb: mental barbel
MC: mental cartilage
Ob 1–3: obliquus muscle (1st–3rd gillarches)
PhCA and P: external and internal pharyngocleithralis muscles
PIM: posterior intermandibularis muscle
PIMm: lateral muscle bands of posterior intermandibularis muscle
PIMms: posterior muscle slips of posterior intermandibularis muscle
PIMt: tendinous portion of posterior intermandibularis muscle
POp: preoperculum
PrH: bony process from second hypobranchial
Q: quadrate
R: rectus muscle
RC: rectus communis muscle
S: sulcus between posterior intermandibularis and interhyoideus muscles
Sc: lateral line sensory canal in dentary
SH: sternohyoideus muscle
SHl: sternohyoideus, lower division
SHu: sternohyoideus, upper division
SHhy: superior hyohyoideus muscle
SOpBr: subopercular branchiostegal rays
T: teeth
THy: tendon from interhyoideus muscle
THy l: tendon from lateral division of interhyoideus muscle
TSH: tendon from sternohyoid
TSHBb: tendon from sternohyoid muscle to second basibranchial
Uh: urohyal
I–V: gill arches

Family **HIODONTIDAE**

Hiodon alosoides (Rafinesque)

(Text-fig. 1A)

Protractor hyoideus complex (text-fig. 3). Although at first sight there appears to be only a single muscle forming the floor of the mouth, closer examination of fibre direction shows that it is a compound of: (1) a large posterior sheet (fibres running obliquely anteromedially towards the median aponeurosis) (2) a much smaller, oval sheet anteriorly (fibres transverse to postero-medial) and (3) on each side, joining the former two sheets, a narrow elongate muscle with almost longitudinally directed fibres.

The various components are tightly joined through narrow aponeuroses, and there is some exchange of fibres between the different muscles.

The posterior sheet originates on the ceratohyal, with a few fibres stemming from the bases of the fourth and fifth branchiostegal rays; a fine median aponeurosis is visible along the entire length of the muscle. A sheet of dense connective tissue joins the lateral margins of this muscle to the ventral margin of the dentary on each side. Anteriorly the muscle ends aponeurotically on a broad sheet of connective tissue extending between the rami of the jaw, and lying dorsal to the other muscles of the protractor hyoideus complex. The posterior sheet joins, aponeurotically, the oval median muscle and, on each side, the slender elongate muscles. Thus, it has no direct insertion onto the lower jaw. In contrast, both the median oval and the lateral rectangular muscles attach directly to the median ventral face of each dentary.

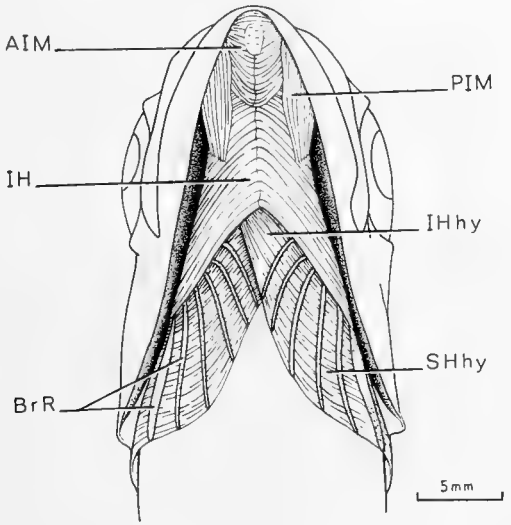


FIG. 3. *Hiodon alosoides*: ventral hyoid muscles after removal of the skin.

From its innervation (a branch of the hyohyoideus VII nerve) and its origin on the ceratohyal, I would identify the posterior muscle sheet as the conjoined left and right interhyoidei. The anterior complex of three muscles (all innervated by a branch of the mandibular V nerve) would seem to be, from their topographical positions, an unpaired median anterior intermandibularis (the oval muscle) and a posterior intermandibularis divided by the backward extension of the anterior intermandibularis.

There is a striking similarity between the protractor hyoideus complex in *Hiodon* and the condition found in *Amia*, *Elops* and *Megalops* (personal observations on *A. calva*, *E. saurus* and *M. cyprinoides*; also Allis, 1897; and Liem, 1967). In all, there is a single anterior intermandibularis, paired (but medially joined in *Amia* and in the elopoid genera) posterior intermandibulares (the geniohyoideus of Liem *op. cit.*), and an extensive, paired interhyoideus. *Hiodon* differs from the others chiefly in having the interhyoid components more compact and closely associated with each other. Liem (*op. cit.*) describes musculose insertions of all components onto the gular plate, but I was unable to confirm this in my own dissections. Indeed, the muscles seem to be completely free from the gular plate which is attached only to the connective tissue covering the muscles. The protractor hyoideus in all four genera differs markedly from that in *Albula* (personal observations; see also Holmquist, 1911; Liem, *op. cit.*), which represents a relatively specialized condition (see also p. 44 for further comments on *Albula* and *Gymnarchus*).

Hyohyoideus. The superior (interbranchiostegal) part of this muscle is weakly developed, and is largely tendinous (text-fig. 3). The inferior part is much better developed. It originates on the first (*i.e.* lowermost) branchiostegal ray of each side and inserts, mainly, on the hypobranchial of the opposite side (left muscle lying below the right). From the medial side of each inferior hyohyoideus a short slip of muscle inserts, through a long shared tendon, onto the basihyal plate about half way along its length. The tendon is closely applied to the ventral face of the basihyal plate even before its actual point of insertion.

Sternohyoideus (text-fig. 4). The main, ventrally situated part of this muscle inserts directly onto the urohyal, and has its origin aponeurotically, from the ventral body musculature. No ventral part of the sternohyoid originates on the cleithrum, but there is a smaller dorsal component originating on the horizontal limb of that bone. From about the middle of this upper segment a broad-based, almost completely tendinous slip runs forward and upwards to insert on the basibranchial of the second gill arch. Apart from this link, there is no connection between the sternohyoideus and the branchial skeleton. The possible significance of this tendon in the evolution of the tendon-bones and ventral bony processes associated with the second gill arch in all other osteoglossomorphs (see Greenwood, Rosen, Weitzman, and Myers, 1966; Nelson, 1968) will be discussed later (page 51).

Ventral gill arch muscles (text-fig. 4). Well-developed *obliqui* muscles are present on the first three gill arches. The *rectus communis* is a large muscle at its origin from the ceratobranchial of the fourth arch, but it becomes tendinous as it passes below the medial end of the second obliquus, and remains tendinous until its insertion on the second basibranchial. This tendon also attaches to a small process from the

second hypobranchial, and is very closely associated with, but distinct from the ligament joining the first basibranchial to the second hypobranchial. A poorly-defined *rectus* is present between the fourth ceratobranchial and the third hypobranchial; it is barely distinguishable from the larger and laterally situated rectus communis. Well developed *anterior* and *posterior transversi* link the proximal ends of the fourth and fifth ceratobranchials respectively.

External and internal *pharyngocleithrales* are present. The origin of the external division is medial to the sternohyoideus, but the internal muscle originates from the cleithrum at the same level as the sternohyoideus, and superficially resembles a division of that muscle.

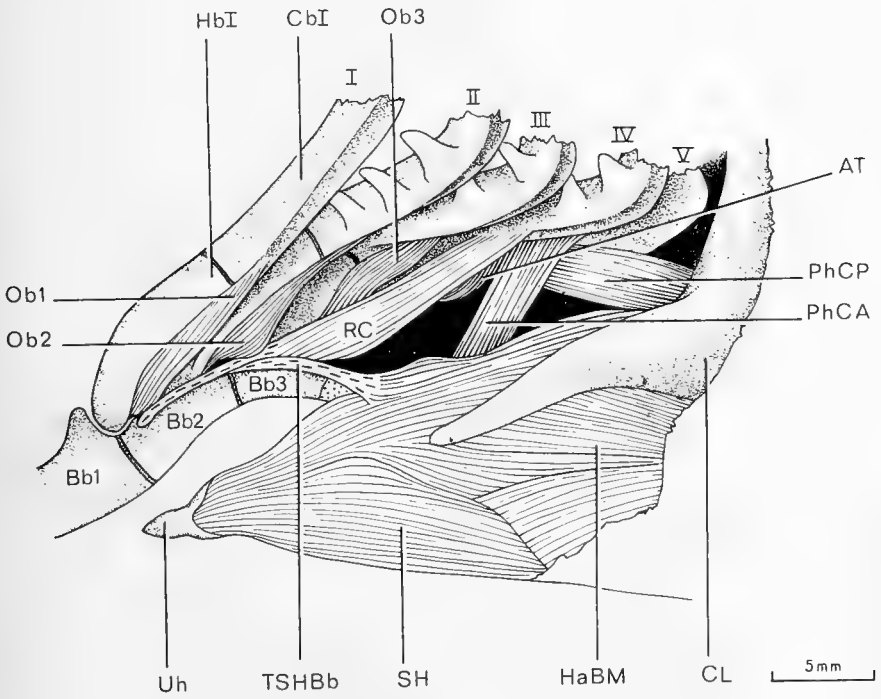


FIG. 4. *Hiodon alosoides*: ventral gill arch musculature and sternohyoideus in left lateral view.

Family **OSTEOGLOSSIDAE**

Subfamily **OSTEOGLOSSINAE** (Nelson, 1968)

Osteoglossum bicirrhosum Vandelli

(Text-fig. 1B)

Protractor hyoideus: is a stout muscle, unpaired except posteriorly over its origins (on each ceratohyal and, in part, aponeurotically from the inferior hyohyoideus of each side). It inserts, through a very short tendinous portion, onto the anterior part of the dentary around the symphysis. This anterior section of the muscle is split, horizontally, by the passage of a stout, transversely aligned *anterior intermandibularis*; that part of the protractor lying above the intermandibularis is thicker.

There is no median longitudinal aponeurosis, but there is a distinct tendinous inscription running transversely at about the middle of the muscle.

Holmquist (1911) and, later, Edgeworth (1935, fig. 277) described the muscle as divided horizontally into a broader, dorsal, *interhyoideus* portion, and a narrower, ventral (and medial) *posterior intermandibularis* portion; both authors also figure the transverse inscription. Despite careful dissection and probing, I could not find any such horizontal division in the muscle. Indeed, in the two specimens I dissected (28·6 and 34·0 cm standard length) the muscle could better be interpreted as being transversely and vertically divided. For example, that section lying anterior to the inscription is innervated by a branch of the mandibular V nerve, but most of the muscle behind the inscription is supplied by a branch of the hyohyoideus VII. This would seem to imply that the anterior part is derived from the posterior intermandibularis, and the posterior part from the interhyoideus However, since the inscription does not penetrate deeply into the muscle (*i.e.* it is not a complete, plate-like aponeurosis) and because the branch of the trigeminal nerve extends behind it, I would not be prepared to delimit the component parts on adult morphology alone. My uncertainty is reinforced by the condition of the muscle in *Pantodon buchholzi* (see page 16), where it seems to approach closely the condition described by Holmquist for *Osteoglossum bicirrhosum*.

Hyohyoideus. The superior portion (between the branchiostegal rays) is moderately developed. The inferior portion, although narrow, is fully muscular. It originates entirely from the first branchiostegal ray and has a tendinous insertion mainly onto the hypohyal of the opposite side; a few fibres, however, have a tendinous insertion onto the hypohyal of their own side. (It may be noted that Holmquist [1911, fig. 11] shows the right inferior hyohyoideus overlapping the left, but in all specimens I have examined [and in all other osteoglossids] left overlaps right).

Sternohyoideus (text-fig. 5). The greater part of this muscle originates on the dorsal surface of the horizontal limb of the cleithrum; a small part stems from the anterior tip of the conjoined cleithra. The sternohyoideus inserts onto the urohyal, but that part passing below the first gill arch is closely attached to the hypobranchial

by a thick connective tissue fascia. The muscle is also closely attached to the inner aspect of the ventrally directed bony processes on the second hypobranchials; each process is, however, entirely superficial to the muscle.

Ventral gill arch muscles (text-fig. 5). *Obliqui* muscles (linking cerato- and hypobranchial elements) are present on the first three gill arches. A small *rectus* muscle connects the fourth ceratohyal with the third hypobranchial.

No *rectus communis* is developed.

The proximal ends of the fourth and fifth ceratobranchials are joined, respectively, by the *anterior and posterior transversi*. The fifth ceratobranchial is also connected to the cleithrum by the strong external and internal *pharyngocleithrales*. The internal pharyngocleithralis is subdivided into a narrow posterior and a much broader anterior part. Both pharyngocleithrales have their origins medial to the sternohyoideus.

Scleropages leichardti Günther

(Text-fig. 1C)

In most details, the musculature of *S. leichardti* is identical with that described for *Osteoglossum bicirrhosum*. Comments made above on the morphology of the protractor hyoideus muscle and its components apply equally to the muscle in *Scleropages*.

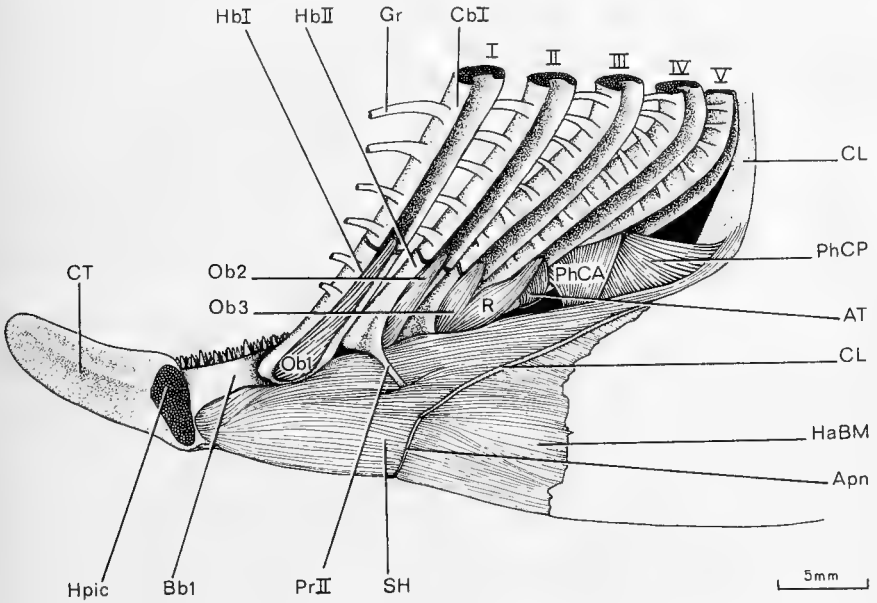


FIG. 5. *Scleropages leichardti*: ventral gill arch muscles and sternohyoideus in left lateral view. The hypohyal has been partly cut away.

Among the ventral gill arch muscles, the only intergeneric difference noted was that in *Scleropages* the proximal end of the rectus muscle is fused with the hypobranchial head of the obliquus of the third arch (text-fig. 5).

Subfamily **HETEROTINAE** (Nelson, 1968)

Heterotis niloticus (Cuvier)

(Text-fig. 1D)

Protractor hyoideus. This stout muscle originates on the ceratohyal and lower three branchiostegal rays of each side, but is a single element over its anterior half. It inserts directly, through short left and right heads, on either side of the dentary symphysis. Slightly anterior to the point of fusion between left and right halves, there is a very distinct transverse inscription; no other division of the muscle can be detected by dissection. The anterior part of the protractor is supplied by a branch of the mandibular V nerve, the posterior part by a branch of the hyohyoideus VII. The latter branch emerges from the medial side of the branchiostegal membrane at the base of the first ray; the main nerve continues forward, and supplies the inferior hyohyoideus muscle.

Heterotis is unusual in having a strong connective tissue link between the protractor hyoideus and the hypohyals (at a point near the union of the protractor's two halves).

A small and narrow *anterior intermandibularis* lies dorsal to the protractor hyoideus and does not pass through any part of it (*cf. Osteoglossum* and *Scleropages*).

Sternohyoideus. This stout muscle originates almost entirely from the dorsal surface of the horizontal limb of the cleithrum; a few ventral fibres stem from the anterior tip of that bone. It inserts onto the urohyal but is also firmly attached to the hypobranchial of the second arch and, less intimately, to the first hypobranchial as well. The ventral processes from the second hypobranchials are partly buried in the sternohyoid.

Ventral gill arch muscles. The most outstanding feature of these muscles is the development of a *rectus communis* from the fourth ceratobranchial to the base of the process on the second hypobranchial; there is also a tendinous connection between this muscle and the third hypobranchial.

In all other respects the gill arch muscles (including the *rectus*) are like those of *Osteoglossum* and *Scleropages*. The *pharyngocleithrales* of *Heterotis*, however, are simpler since the internal muscle is undivided.

Arapaima gigas (Schinz)

(Text-fig. 1E)

Protractor hyoideus: is a short, largely paired muscle originating from the ceratohyal and the basal parts of the second and third branchiostegal rays. Only about

the anterior third of the muscle is unpaired, the two halves meeting along a weak aponeurosis. Slightly anterior to this junction there is a transverse tendinous inscription.

The protractor inserts, through left and right musculose heads, on either side of the dentary symphysis. A small and narrow *anterior intermandibularis* passes through the muscle a little posterior to its insertion.

It is impossible, by inspection or dissection, to determine the extent of the protractor's component muscles, nor is it possible to determine the manner of their fusion.

Hyohyoideus. The superficial part is moderately well-developed and largely muscular. The inferior division is short and relatively stout; it inserts through a long tendon onto the hypohyal of the opposite side.

Sternohyoideus. Undoubtedly the sternohyoideus is the most characteristic muscle of *Arapaima gigas* (see text-fig. 6). It is divided, horizontally, into a small anterior and dorsal division, and a much larger unpaired ventral part. The latter originates (as is usual) on the horizontal limb of the cleithrum, and inserts on either side of the peculiarly shaped urohyal. In cross-section, this bone is shaped like an inverted T, with the arms extended to such a degree that the anterior half of the lower sternohyoid is completely covered by bone. A broad ligament from either side of the urohyal attaches it, ventrally, to the ceratohyals and hypohyals. The small ventral process of the second hypohyal barely contacts the dorsal part of this ventral sternohyoid division. Indeed, the process in *Arapaima* is the shortest found in any osteoglossid, and has the least intimate contact with the sternohyoid.

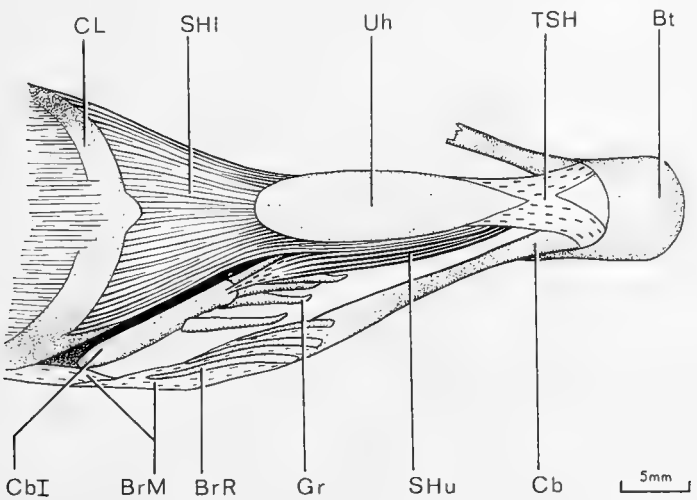


FIG. 6. *Arapaima gigas*: ventral view of the sternohyoid, to show its upper and lower divisions and their relationship with the urohyal, cleithrum and first hypobranchial. Semi-schematic; the lower jaw is not depicted. Cb=ceratohyal.

The dorsal division of the sternohyoid is paired. Each half originates on the ventral face of the first hypobranchial, and extends over almost the entire length of that bone (thus underlying the first obliquus muscle). The left and right halves meet, aponeurotically, in the midline; the broad tendon originating at this union inserts, somewhat asymmetrically, on the inner aspect of the ceratohyals near their tips. Although some part of the tendon inserts on the right ceratohyal, by far the greater part is attached to the left bone.

No other osteoglossid shows such clear-cut subdivision of the sternohyoid, or such asymmetry in its insertion. In fact, insertion of even part of the sternohyoid onto the ceratohyals is most unusual in teleosts. Nevertheless, it is difficult to identify the upper division of this muscle in *Arapaima* as other than part of the sternohyoideus. That other osteoglossids have a close association of the sternohyoid with the first and second hypobranchials, and that there is an incipient division of the muscle in *Heterotis* (see p. 14), all seem to support the recognition of a divided sternohyoid in *Arapaima*.

Ventral gill arch muscles: in *Arapaima* have the typical osteoglossid pattern; there is no *rectus communis*.

Obliqui are present on the first three arches; the obliquus of the third arch is closely associated with the well-developed *rectus* running almost in the midline from the fourth ceratobranchial to the third hypobranchial. Anterior and posterior *transversi* are present, as are stout and undivided internal and external *pharyngocleithrales*.

Family **PANTODONTIDAE**

Pantodon buchholzi Peters

(Text-fig. 1F)

Protractor hyoideus (text-fig. 7): is a single muscle over its anterior half, but is paired posteriorly, with the left and right halves originating on the ceratohyal and lower three branchiostegal rays of their side.

The muscle is marked by a transverse inscription at the point where the two halves unite. At this point, the unpaired portion is visibly separable into a broad dorsal section (inserting on either side of the dentary symphysis) and a much narrower, more compact, median and ventral part which inserts, tendinously, onto the symphysis itself. Slight pressure with a probe along the horizontal sulcus demarcating the two parts separates them back to the level of the transverse inscription. Beyond this point there is considerable interchange between the parts, and the sulcus itself is no longer distinct.

A well-developed, stout, transverse *anterior intermandibularis* lies between, and separates, the dorsal and ventral parts of the protractor anteriorly.

In many respects, the condition of the protractor hyoideus in *Pantodon* resembles that described for *Osteoglossum* by Holmquist (*op. cit.*) and Edgeworth (1935); it will be recalled that I found a rather different arrangement in that genus (see p. 12).

Pantodon differs from Holmquist's description of *Osteoglossum* in that the muscles cannot be separated posteriorly beyond the transverse inscription. Holmquist and Edgeworth identify the entire length of the median, ventral section of the muscle in *Osteoglossum* as a protractor hyoideus (*i.e.* a posterior intermandibu aris in the terminology used here), and the overlying, broader part as the interhyoideus component.

Identifying the components of the protractor hyoideus in *Pantodon* is not easy, particularly since the innervation cannot readily be traced within the muscle. Judging from the position of the upper and lower insertions, and from the fact that the ventromedial segment is so clearly circumscribed, I would identify it as the posterior intermandibularis; the much larger muscle above, lateral to and behind it would then be the interhyoideus portion. In other words, a situation like that in the protractor hyoideus of *Salmo salar* (see Holmquist, 1911, and Dietz, 1912).

Hyohyoideus. Both the superior and inferior divisions are well-developed, the latter originating on the first branchiostegal ray, and inserting tendinously on the hypohyal of the opposite side.

Sternohyoideus. The lower third of this muscle originates on a broad aponeurosis with the ventral body musculature; the remainder stems from the dorsal surface of the horizontal limb of the cleithrum. Anteriorly, the sternohyoid inserts around the small urohyal which is completely embedded in the muscle. The medial face of

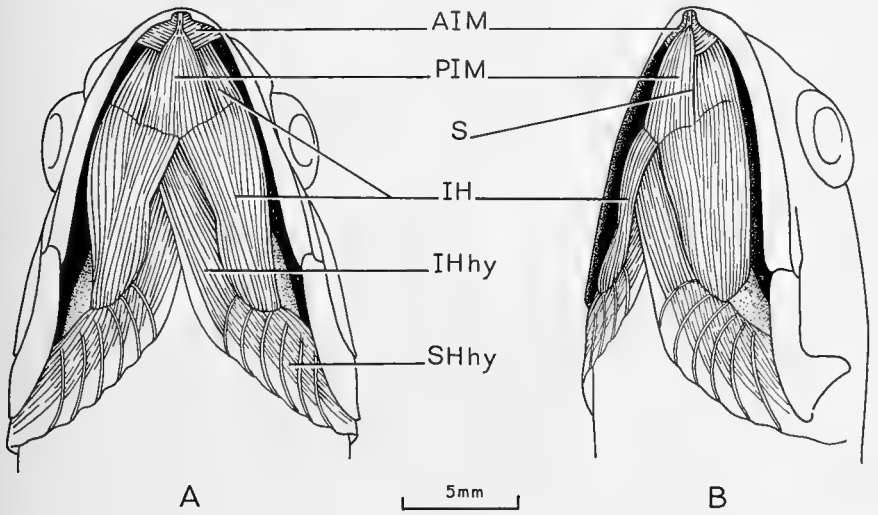


FIG. 7. *Pantodon buchholzi*: ventral hyoid musculature. A. In ventral view. B. In oblique ventro-lateral view. The transverse inscription (aponeurosis) is shown, but not labelled, in both views.

each process from the second hypobranchial is firmly but superficially attached to the sternohyoid, which is also closely attached by connective tissue to the ventral side of the first hypobranchial.

Ventral gill arch muscles. As in *Heterotis* (but not other osteoglossids) a distinct *rectus communis* is present; the small *rectus* from the fourth ceratobranchial to the third hypobranchial is distinct from the rectus communis but is closely applied to it. *Obliqui* are present on the first three arches; anterior and posterior *transversi* are well developed, and the pharyngocleithrales are simple but relatively stout.

Family **NOTOPTERIDAE**

Munshi has given a detailed description of the cranial muscles in the Asiatic species *Notopterus chitala*, and Nelson (1969) has listed the branchial muscles of the same species. In view of this previous work, I have concentrated on the two African species, *Papyrocranus afer* and *Xenomystus nigri* (see also Greenwood, 1963 and Nelson *op. cit.*). Some comments on Munshi's description of the hyoid muscles in *N. chitala*, and a general comparison of the hyoid and gill musculature in the three genera follow the separate accounts for *Papyrocranus* and *Xenomystus*.

Papyrocranus afer (Günther)

(Text-fig. 1G)

Ventral hyoid musculature (text-fig. 8). The most superficial (*i.e.* ventral) muscle has its origin, on each side, equally from the ceratohyal and from the basal part of branchiostegal rays 2 to 6. The two halves of this muscle join to form a single element over about the anterior half of their length.

Anteriorly, the muscle inserts onto the dentary through dorsal and ventral heads; the single, narrow and tendinous ventral insertion is onto the symphysis, while the broader, more musculose dorsal insertion is double and lies on either side of the symphysis.

This ventral muscle is innervated solely by a branch of the mandibular V nerve. Careful dissection shows that no branch of the hyohyoideus VII runs to it (see below under *interhyoideus*).

With respect to its innervation, the muscle differs from the topographically similar muscle (the protractor hyoideus) in osteoglossid and pantodontid fishes. Munshi (*op. cit.*) identifies the muscle in *Notopterus* as a *posterior intermandibularis* and I would agree with his identification, both on the grounds of the muscle's innervation solely from the trigeminal nerve, and because distinct interhyoideus muscles (innervated from the facialis nerve) are also present. It will be recalled

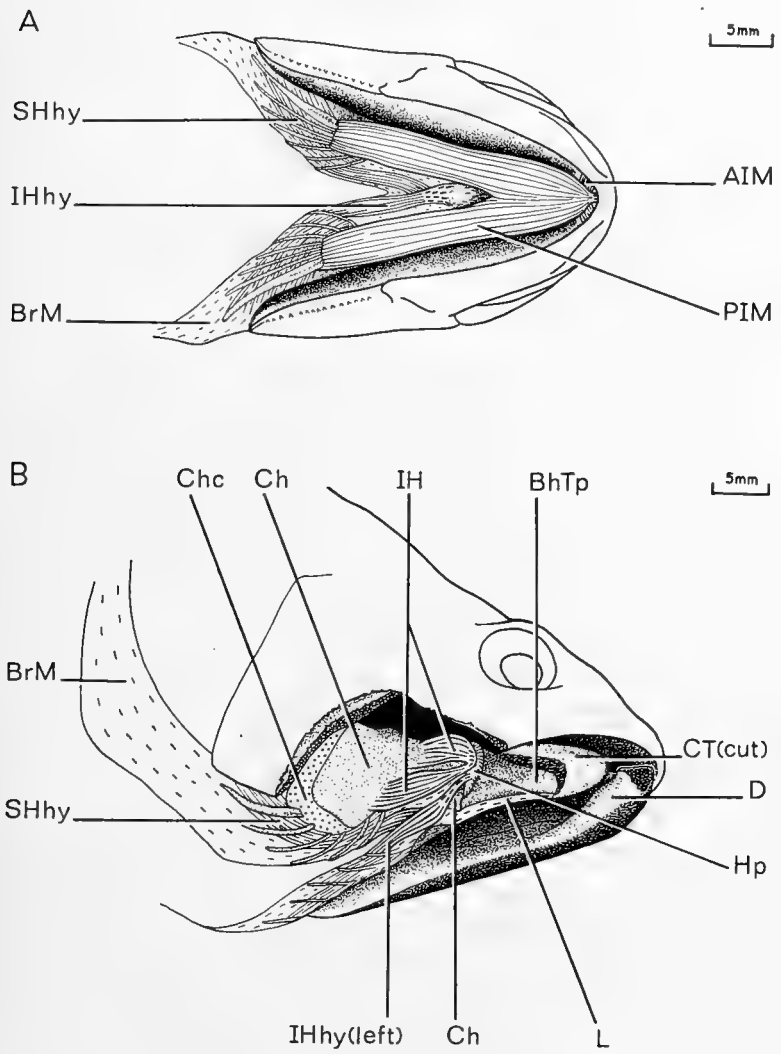


FIG. 8. *Papyrocranus afer*: A. ventral hyoid muscles, after removal of the skin. B. ventro-lateral view of head to show the interhyoideus muscles. The right half of the lower jaw removed, as is the cheek and jaw musculature of that side.

that in osteoglossoids the protractor hyoideus has a double (trigeminal and facialis) innervation, and that in these fishes no separate interhyoideus is present.

A small and weak *anterior intermandibularis* muscle lies between the dorsal and ventral insertions of the posterior intermandibularis. Its fibres are transversely orientated, and attach to the median face of the dentary on either side of the symphysis.

Interhyoideus (text-fig. 8). This paired muscle appears to be further divided on each side into a shallow lower portion, and a deeper upper part (see fig. 8B). Anteriorly, however, the two parts have a common tendinous insertion onto the dorsal surface of the hypohyal of the same side. The upper division originates entirely from the ceratohyal, but the lower part originates from the ventral margin of the ceratohyal and, in minor part, from the heads of the first two branchiostega. rays. The interhyoideus is innervated by a branch of the hyohyoideus VII nervel This nerve enters the lower muscle division after emerging from behind the branchiostegal rays and passing along the upper margin of the first ray.

Hyohyoideus. The superior division is rather poorly developed, and is almost completely tendinous. The inferior part is also tendinous but has its medial third strongly muscular (fig. 8B). This muscular section originates from the distal third of the first branchiostegal ray. The whole inferior hyohyoid inserts, tendinously, on the hypohyal of the opposite side (the left muscle passing ventral to the right).

Sternohyoideus (text-fig. 9). The large sternohyoideus originates entirely from the dorsal surface of the horizontal limb of the cleithrum. Ventrally, part of the muscle inserts, through a pair of tendons, onto the hypohyals and the anteroventral tip of each ceratohyal (a most unusual arrangement; see also *Arapaima*, page 15). However, the bulk of the sternohyoid inserts onto and around the small urohyal which is completely embedded in the muscle. (It should be noted that a pair of strong ligaments from the ventral face of the basihyal tooth-plate also attach to the urohyal and are, in consequence, partly covered by the sternohyoid.)

The median face and posterior margin of each ventral process (tendon bones) from the second basibranchial are firmly but superficially attached to the lateral face of the sternohyoid on each side. Anterior to this point the muscle closely approaches the first basibranchial but is not attached to it.

Ventral gill arch muscles (text-fig. 9) Well-developed *obliqui* are present on the first three gill arches; the muscles of all three arches insert on the respective ceratobranchial, but those on the first and second arch have a double origin, from the hypo- and basibranchial.

A distinct *rectus* runs from the third hypobranchial to the ceratobranchial of the fourth arch where it comes into close contact with the head of a stout *rectus communis* connecting that arch with the base of the ventral process (tendon bone) articulating with the second basibranchial.

The prox mal ends of the fourth and fifth ceratobranchials are joined, respectively, by the broad *anterior* and *posterior transversi.*

The external and internal *pharyngocleithrales* are well-developed, simple muscles whose origins lie medial to the sternohyoideus.

Xenomystus nigri (Günther)

(Text-fig. 1H)

In all major details the musculature of this species is like that of *Papyrocranus afer*. The most noticeable differences may be listed briefly.

Posterior intermandibularis. The origin is mainly from the ceratohyal, with only about one quarter stemming from the first branchiostegal ray. It inserts through a single broad head, an arrangement possibly correlated with the much weaker and rather ill-defined *anterior intermanibularis* in this species. As in *Papyrocranus* the posterior and anterior intermandibulares are innervated by a branch of the mandibular V nerve.

Hyohyoideus. The inferior divisions fuse in the midline before inserting onto the hypohyals.

Interhyoideus: in this species is a pair of undivided muscles fused anteroventrally, and inserting onto the hypohyals through a short tendon which wraps around the face of these bones.

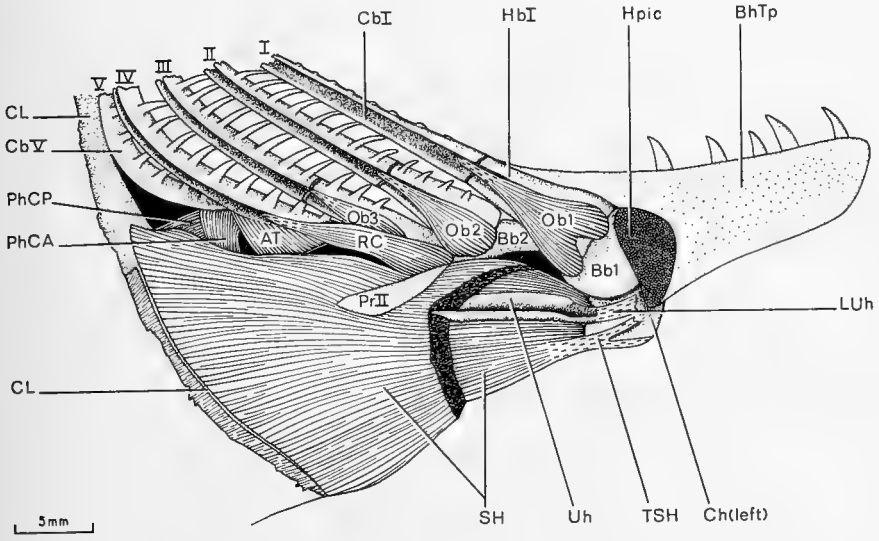


FIG. 9. *Papyrocranus afer*: lateral view of gill arch muscles and sternohyoideus. The anterior part of the sternohyoid has been dissected away on the right side to show the embedded urohyal. The tendon (TSH) inserts onto the right ceratohyal (removed) and right hypohyal (partly removed).

Gill arch muscles. I was unable to locate a separate *rectus* in *Xenomystus.* The *rectus communis* is present and large; like the *obliqui* it appears to be relatively larger in this genus. As in *Papyrocranus,* the obliqui of the first two arches originate from both the hypo- and the basibranchials.

PAPYROCRANUS AND *XENOMYSTUS* COMPARED WITH *NOTOPTERUS*

Basically, the musculature in the three genera is very similar (see Munshi, 1960 for *Notopterus*). In the two *Notopterus* species I examined (*N. chitala* and *N. kapirat*), the interhyoideus of each side is undivided (*i.e.* like that of *Xenomystus*); in *N. kapirat* it is indistinguishable ventrally from the upper, anterior part of the inferior hyohyoideus. According to Munshi (*op. cit.*) the left and right interhyoidei of *N. chitala* fuse medially. But, in his figure the muscles are shown as fan-like, horizontally disposed structures continuous with the inferior hyohyoidei, and running obliquely towards the midline; here the posterior portion of the left interhyoideus overlaps that of the right muscle. In the single specimen I dissected, the interhyoidei are vertically aligned (as in the other species considered), insert separately and are quite distinct from the inferior hyohyoidei. In other words, a situation identical with that found in *Papyrocranus.*

I would contest Munshi's identification of the muscle running from each basibranchial process (tendon bone) to the urohyal. This he calls the pharyngohyoideus (= rectus communis in the nomenclature used above). However, the figure shows the muscle as only partly distinct from the sternohyoideus (Munshi's rectus cervicus) below it, and no fibres are shown connecting with the upper posterior face of the tendon bones (as do those of the rectus communis). In the specimen I have examined (as in *N. kapirat, Papyrocranus* and *Xenomystus* also) it is not possible to separate the fibres attached to the tendon bone from those of the underlying sternohyoid. In contrast, the muscle I have identified as a rectus communis is distinguishable from the sternohyoideus even at its insertion onto the tendon bone where the two muscles are closely apposed. Thus it seems likely that the muscle Munshi identifies as a rectus communis is, in fact, part of the sternohyoideus.

Family **MORMYRIDAE**

The bauplan of the hyoid and gill arch musculature is remarkably constant in the Mormyridae, despite the great range of variation in head shape and jaw form of these fishes. The more outstanding features of the mormyrid musculature may be summarized as follows:—

(i) The muscles of the *protractor hyoideus complex* show the greatest degree of individuality and subdivision of any osteoglossomorph fishes; the interhyoideus muscles are enlarged and insert onto the lower jaw.

(ii) There is considerable hypertrophy of the *hyohyoideus* with the consequent loss of distinct superior and inferior divisions; the left and right halves of the muscle

join medially and the muscle is attached to the interopercula and ceratohyals as well as to the urohyal. This specialized musculature is associated with the peculiar branchial specializations of all mormyrids. For example, there is no discrete and expandible branchiostegal membrane, the rays being buried in the hyohyoideus, and the whole mass covered by skin continuous with that of the body; in consequence, the opercluar aperture is greatly restricted and lies entirely above the branchiostegal rays.

(iii) In the ventral gill arch musculature the *obliqui* have extensive areas of attachment, and the weakly developed *pharyngocleithrales* lie external to the sternohyoideus. The anterior part of the *sternohyoideus* is closely associated with the corresponding ventral elements of the gill arches, although there is never a direct musculose or tendinous insertion onto these bones.

Surprisingly, little attention has been paid to the cephalic and branchial musculature of mormyroid fishes. Holmquist (1911), drawing on his investigation of the hyoid musculature in *Gymnarchus niloticus*, noted certain peculiarities, but he was unable to extend his observations because of lack of comparative material. Nelson (1969) briefly commented on the gill arch muscles in Mormyridae and compared these with those of other osteoglossomorphs. The most comprehensive treatment is that of Bishai (1967) on *Mormyrus caschive*. Unfortunately, the nomenclature used by this author makes direct comparison very difficult, and I suspect that his description of the gill arch musculature is erroneous in many respects (see below, page 28).

Since the bauplan of the hyoid and ventral gill arch muscles is so similar in all mormyrids, I shall give a detailed description for one species only; deviations from this pattern will be noted for the other species examined.

Mormyrus kannume Forsk.

(Text-fig. 2A)

The snout in this species is slender, moderately decurved, produced and tubular, with the mouth small and terminal.

Posterior intermandibularis (text-fig. 10A): is a fairly thick muscle with originates, aponeurotically, over the anterior part of the hyohyoideus, and directly from the interoperculum of each side. It inserts through two muscular heads on either side of the mental cartilage (that is, it does not attach directly to the dentary). At about its midpoint there is a faint, longitudinal aponeurosis which extends anteriorly; posterior to this point both halves of the muscle are contiguous medially throughout their lengths. The posterior intermandibularis is broad and extends laterally almost to the ventral margin of each dentary, to which it is attached by a connective tissue sheet.

Anterior intermandibularis (text-fig. 10B): lies immediately above the posterior division. It is a relatively thin but expansive muscle extending longitudinally from the level of the posterior interopercular margin to a little behind the mental cartilage.

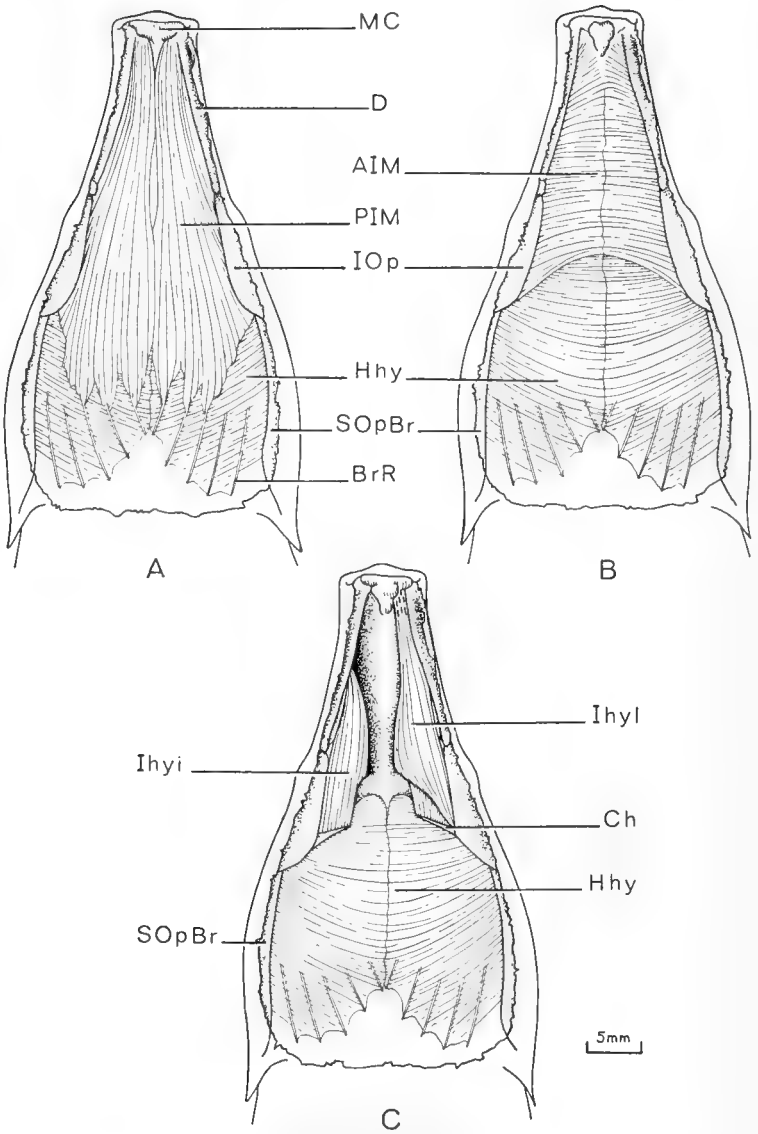


FIG. 10. *Mormyrus kannume*: ventral hyoid muscles. A. After removal of the skin. B. Posterior intermandibularis removed. C. Anterior intermandibularis removed; right lateral division of the interhyoideus muscle removed.

Laterally it inserts, directly, onto the interoperculum, articular and the dentary. All its fibres are transversely arranged; there is a faint but distinct median aponeurosis extending along the entire length of the muscle.

Both the anterior and posterior intermandibularis are innervated by a branch of the mandibular V nerve.

Interhyoideus (text-fig. 10C). A bilaterally paired muscle originating on the hyoid arch but inserting on the medial face of each dentary and articular, is identified as the interhyoideus because of its origin (the epi- and ceratohyal) and because of its innervation (a branch of the hyohyoideus VII).

The lateral (*i.e.* outer) muscle of each pair is the larger; it has a narrow origin from the upper part of the ceratohyal and part of the epihyal, and inserts tendinously onto the ventral margin of the dentary immediately lateral to the symphysis.

The inner and smaller muscle has a much wider origin (entirely from the ceratohyal) ventral to that of the lateral division. It inserts on the medial face of the dentary, and also the articular, considerably behind and above that of the outer division.

Hyohyoideus (text-fig. 10): is a stout, thick muscle with the left and right halves meeting medially along a fine aponeurosis. The branchiostegal rays are almost completely embedded in muscle; it is impossible to recognize separate superior and inferior divisions. The posterior part of the hyohyoideus is attached to the subopercular branchiostegal rays,[1] the middle section to the interoperculum, and the forward part to the anterior face and ventral margin of the ceratohyal laterally; medially the muscle is attached to the urohyal. All these connections are musculose.

Externally, the hyohyoideus is covered by skin which is continuous with that of the body and lower surface of the jaw. In other words, there is no separate branchiostegal membrane. Internally, the medial face of the hyohyoideus is bound to the overlying ventral body musculature by an extensive connective tissue union.

Sternohyoideus: is a large muscle originating mainly from the dorsal face of the horizontal cleithrum, but with a small ventral portion continuous with the hypaxial body muscles. The sternohyoid inserts on the urohyal but its antero-dorsal section is closely associated, through a connective tissue fascia, with the second basibranchial. The ventral processes from the second hypobranchials are, proximally, embedded in the sternohyoid; distally they lie outside the muscle but closely attached to its lateral face.

Ventral gill arch musculature (text-fig. 11). Well-developed *obliqui* are present on the first three gill arches; all are broad muscles extending onto the ceratobranchial well beyond its articulation with the small hypobranchial. From the first obliquus there is a distinct postero-medially directed slip of muscle which inserts onto the second hypobranchial. From the second obliquus a similar slip runs to, and inserts on, the second basibranchial. The third obliquus links only the cerato- and hypobranchial of its arch.

[1]In mormyrids the upper two branchiostegal rays are blade-like bones which have lost their articulation with the hyoid arch. Instead, the two bones are firmly attached to one another, and the upper bone is immovably attached to the lower margin of the operculum. Together, these two rays form an apparently immovable pseudosuboperculum.

A moderately developed *rectus communis* extends between the fourth ceratobranchial and the proximal end of the ventral process from the second hypobranchial. The muscle is closely applied to, but distinct from, the dorsal margin of the sternohyoideus. A short, broad and nearly triangular muscle joins the fourth and fifth ceratobranchials near their proximal ends. I cannot be certain about the identity of this muscle It could be a displaced obliquus of the fourth arch or, more likely, part of this obliquus since there is a large transversus associated with the arch (all this assuming that obliqui are, primitively, associated with each arch; see Nelson, 1967).

The *anterior transversus* is moderately broad; it links the ventral tips of the fourth ceratobranchials. The *posterior transversus* runs obliquely forward so that it has the shape of a V, the apex inserting on the cartilaginous block lying between the ventral tips of the third and fourth ceratobranchials (the fourth basibranchial of Nelson, 1968). The arms of the V are closely applied to the ventral surface of each ceratobranchial.

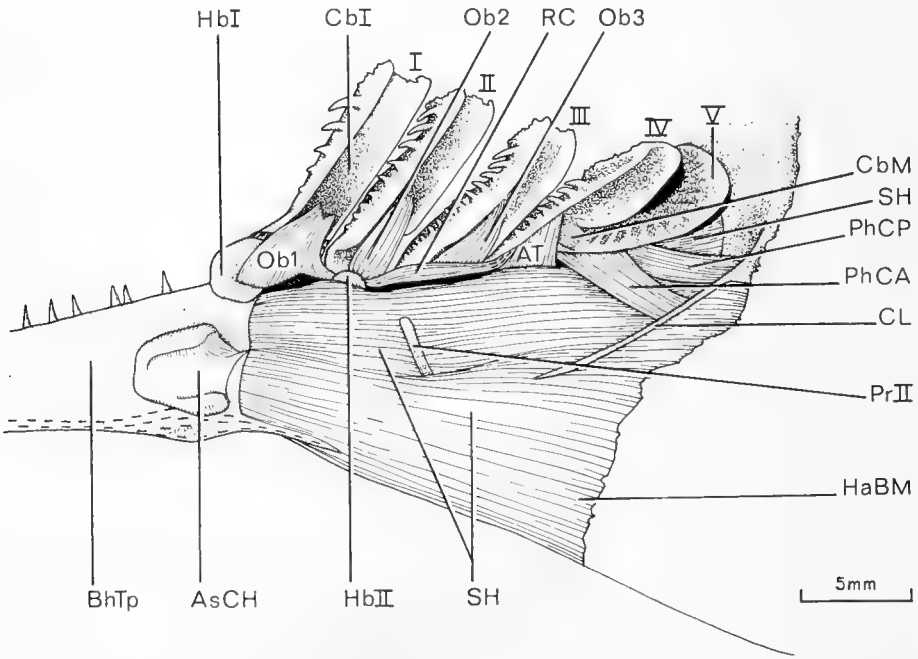


FIG. 11. *Mormyrus kannume*: ventral gill arch muscles and sternohyoideus in left lateral view. Not all the connective tissue surrounding the basihyal and urohyal has been dissected away.

External and internal *pharyngocleithrales* are present, but are not strongly developed. An unusual feature of these muscles in all mormyrids is their origin external to the sternohyoideus Both divisions, but especially the external one, have a deep and broad insertion on the fifth ceratobranchial.

Mormyrus caschive Linn.

(Text-fig. 2B)

Bishai i(1967) has given a detailed account of the cranial and branchial muscles in this species Unfortunately, I have been unable to dissect a specimen, but since in osteologcal and other features *M. caschive* is very similar to *M. kannume*, it seems reasonable to assume that the musculature would also be similar.

Thus, it is surprising to find a number of departures from the *M. kannume* condition in the ventral musculature of *M. cashive* as described by Bishai. Because muscle nomenclature used by this author differs from that usually employed, and because of the anatomical differences noted, I shall give a list of synonyms for the muscles involved and also comment on the apparent discrepancies between my observations on *M. kannume* and Bishai's on *M. caschive.*

In general, I would agree with Bishai's description of the superficial hyoid muscles. His *depressor labii inferioris* muscle is my posterior intermandibularis, and his *intermandibularis* is my anterior intermandibularis. The posterior intermandibularis of *M. caschive* (*cf.* text-fig. 10A with Bishai's fig. 4) is narrower anteriorly and seems to extend further posteriorly, covering the entire hyohyoideus (*i.e.* the *interbranchiostegalis* muscle of Bishai).

There is also substantial agreement in the arrangement of the deep ventral muscles (Bishai's *geniohyoideus internus* and *externus*, which are my inner and outer divisions of the interhyoideus). According to Bishai's figure 5, there are three divisions of this muscle, the innermost of which is not labelled. However, I suspect that the object which Bishai has labelled "geniohyoideus externus" is, in fact, a cut section of skin (or even cheek muscle); further, it seems that his "internus" muscle should be labelled "externus", and that the short unidentified innermost muscle is the internal division of his geniohyoid series (*i.e.* my interhyoid series).

The same figure also shows a condition of the sternohyoideus which I find difficult to accept. However, I think the figure is explicable when one considers Bishai's description of the ventral branchial muscles (*op. cit.*, page 21, and fig. 8). Here the author describes three large muscles, originating on each side from the cleithrum, and inserting on the urohyal and the ventral processes of the second hypobranchials. These muscles are identified by Bishai as "anterior portions of the pharyngoclavicularis muscle". Apart from an abuse of the term pharyngoclavicularis for muscles with these topographical relationships, it seems that Bishai failed to recognize their true identity as parts of the sternohyoideus (see page 25).

Bishai's *pharyngocleithralis posterior* apparently consists of both the external and internal divisions of this muscle.

I cannot find separate muscles in *M. kannume* corresponding to Bishai's *pharyngoarcualis anterior*, and *obliquus ventralis anterior* and *posterior* (of the first gill arch, see his fig. 8). Indeed, it seems that he has misinterpreted the double-headed condition of the first obliquus muscle which inserts, mainly, on the first hypobranchial but also has a slip passing to the second hypobranchial (see page 25).

Bishai does not describe a *rectus communis* muscle but his *fourth obliquus ventralis superioris* could well be part of a rectus communis (*viz.* that portion near its origin on the fourth arch and below the third arch).

Likewise, Bishai's *obliquus ventralis superioris* 5 seems to correspond to the small muscle, present in most mormyrids, which links the ceratobranchials of the fourth and fifth arches (see page 26).

The anterior transversus (*i.e.*, the *fourth transversus ventralis* of Bishai) requires no comment, but I believe that Bishai has misidentified the posterior transversus, and called it the *pharyngoarcualis posterior* (see page 51 for a discussion of the posterior transversus in mormyrids).

Mormyrus lacerda Casteln.

(Text-fig. 2C)

In this species the snout is relatively short, broad and but slightly decurved; the mouth is broad and terminal in position.

With few exceptions, the musculature is like that of *Mormyrus kannume*.

The *anterior intermandibularis* inserts onto the dentary and angular only; over its posterior third it fails to reach the lateral margins of the head. However, its posterolateral tips are attached to the ceratohyal near the origin of the interhyoideus.

The *posterior intermandibularis*, relative to that of *M. kannume*, is somewhat less substantial over its posterior half.

The *pharyngocleithrales* are complex. There are three distinct but contiguous heads on the cleithrum, all originating lateral to the sternohyoideus. At about the midpoint between girdle and ceratobranchial, the three separate muscles fuse, become tendinous and then, as a single element, become muscular again. Presumably this muscle should be considered as fused external and internal pharyngocleithrales.

Mormyrus hasselquisti Val.

(Text-fig. 2D)

In this species the snout is short, broad and but very slightly decurved. The mouth is broad and terminal.

The musculature of *M. hasselquisti* is virtually identical with that of *M. lacerda* (text-fig. 12). The anterior half of the *posterior intermandibularis* is, however, not quite so broad. It is separated from the ventral margin of the articular and dentary by a distinct connective tissue band through which the underlying anterior intermandibularis can be seen.

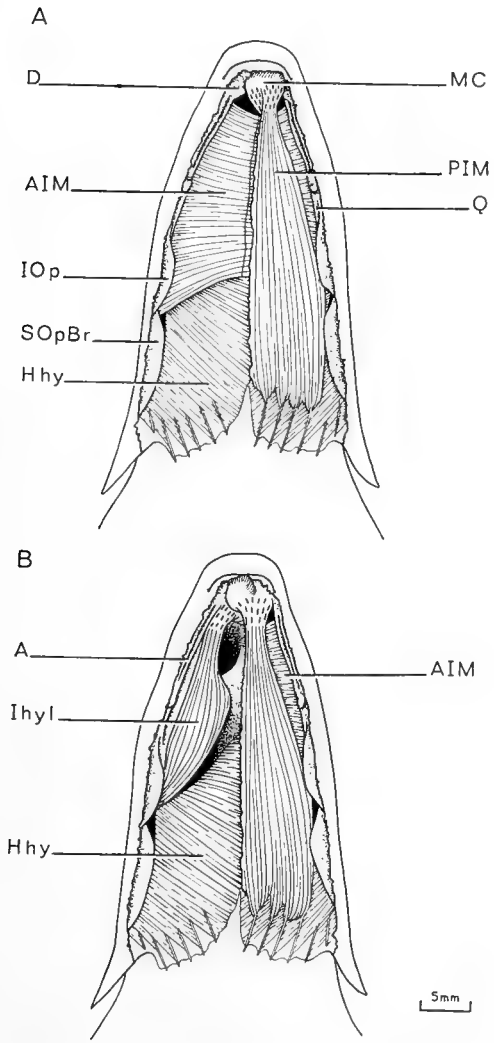


FIG. 12. *Mormyrus hasselquisti*: ventral hyoid muscles. A. Right half of posterior intermandibularis removed. B. Right half of the anterior intermandibularis removed.

Cyphomyrus discorhynchus (Peters)

(Text-fig. 2E)

The snout in this species is short, broad and strongly decurved, with the small mouth situated subterminally and its opening directed somewhat ventrally.

The genus *Cyphomyrus*, once part of the large and probably artificial assemblage of species in the genus *Marcusenius*, was separated out by Myers (1960).

There are several small but none the less characteristic features in the musculature of *C. discorhynchus*.

The *posterior intermandibularis* (text-fig. 13) is well developed, but anteriorly it does not extend to the lateral margins of the lower jaw. That section of the muscle originating on the interoperculum has its fibres more closely packed than are those in the larger section originating from an aponeurosis over the hyohyoideus muscle. The two parts of the intermandibularis can be separated easily by gentle traction.

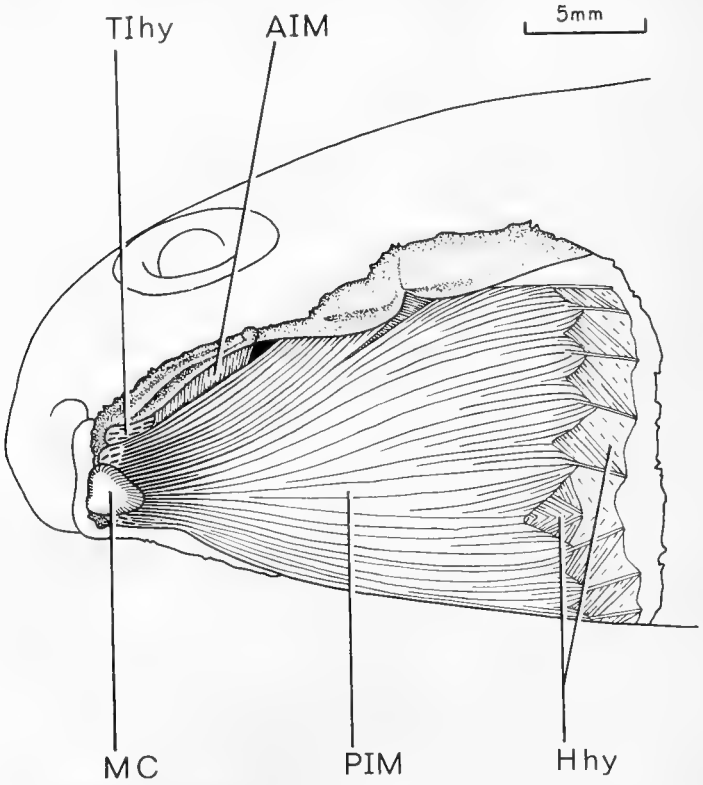


FIG. 13. *Cyphomyrus discorhynchus:* oblique ventro-lateral view of the hyoid musculature, after removal of the skin.

The *anterior intermandibularis* (text-fig. 13) is a short muscle showing some individual variability in length. In only one of the three fishes examined does this muscle extend anteriorly to the level of the posterior intermandibularis insertion; in one fish it extends posteriorly to the interoperculum (to which it is attached), in another it does not quite reach that point, whilst in the third fish, the muscle is attached to the interoperculum on one side but does not contact that bone on the other side. In all three specimens a slip from the posterior margin of the muscle passes upwards on each side to insert on the anterior face of the ceratohyal.

The major part of the *sternohyoideus* originates, aponeurotically, from the ventral body musculature; only a small part of the muscle originates from the cleithrum.

The ventral gill arch musculature is unusual in having, in addition to a *rectus communis*, a short but discrete muscle extending between the ventro-lateral ends of the second and third ceratobranchials.

Marcusenius cyprinoides (Linn.).

(Text-fig. 2F)

This species is usually classified in the genus *Gnathonemus*, but Taverne's (1968) recent investigations have shown that it and other short-snouted species are more properly included in the genus *Marcusenius* Gill as revised by Taverne (of which *M. cyprinoides* is the type species).

The snout of *M. cyprinoides* is relatively short and broad, and is not strongly decurved. The small mouth is terminal in position but has its opening directed somewhat dorsally. There is a noticeable submental protruberence into which the lower lip passes insensibly.

The *posterior intermandibularis* has the typical mormyrid origin from the interoperculum and from above the hyohyoideus. It inserts, however, entirely onto the enlarged submental cartilage; that is, it has no direct connection with the dentary.

The *anterior intermandibularis*, in contrast with that of the other species described above, is greatly reduced in size. Its length is only slightly greater than that of the eye, and it is confined to the articular region of the lower jaw. It inserts onto the articular of each side just before the articular-quadrate joint. The medial section of this muscle is tendinous.

The paired *interhyoideus* muscles, and the hypertrophied *hyohyoideus* are typical.

The *sternohyoideus* originates mainly from the dorsal surface of the horizontal limb of the cleithrum, but a small ventral part arises, aponeurotically, from the hypaxial body musculature. As in other mormyrid genera, the anterior part of the sternohyoid is closely associated with the ventral region of the first two gill arches. The ventral processes from the second hypobranchials are completely embedded in the sternohyoideus.

The *ventral gill arch muscles* are typical (see under *M. kannume*) except that there is, apparently, no short, triangular muscle connecting the fourth and fifth ceratobranchials.

Marcusenius victoriae (Worthington)

(Text-fig. 2G)

This species closely resembles *M. cyprinoides* (and like that species was formerly included in the genus *Gnathonemus*).

The musculature too is virtually identical with that of *M. cyprinoides*, although the *anterior intermandibularis* (text-fig. 14) is a little further reduced in size, and the muscle connecting the fourth and fifth ceratobranchials is present.

Gnathonemus longibarbis (Hilgendorf)

(Text-fig. 2H)

The snout is moderately short (especially as compared with other *Gnathonemus* species; see Taverne [1968]), the mouth small and terminal, and there is a long tubular submental barbel.

The *posterior intermandibularis* is an extensive muscle, originating, as is usual, over the hyohyoideus and from the interopercula. It has strong connective tissue attachments (in which some muscle fibres occur) to the ventral margin of the

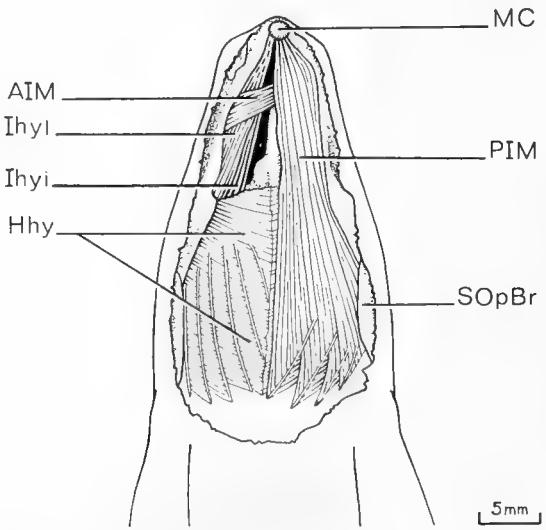


FIG. 14. *Marcusenius victoriae*: ventral hyoid musculature. The right half of the posterior intermandibularis muscle removed to show overlying muscles.

articular, dentary and preoperculum. Anteriorly, the muscle almost completely surrounds the massive, elongate submental cartilage, and reaches to its distal tip. A few fibres attach to the dentary at the base of the cartilage.

There is no trace of a distinct *anterior* (*i.e.* transverse) *intermandibularis*, nor can it be detected as a component of the posterior intermandibularis.

The *interhyoidei* are well developed but the bellies of the medial and lateral muscles on each side are not readily separated. Both divisions have distinct origins and insertions (like those in the species where the bodies of the muscles are distinct).

The *hyohyoideus* is typical (see page 25).

Most of the *sternohyoideus* originates on the cleithrum, but a small ventral portion is continuous with the hypaxial body musculature. As in other mormyrid species, the muscle has an intimate association with the ventral elements of the first two gill arches; the processes from the second hypobranchials are embedded proximally but lie on the surface of the sternohyoid distally.

The ventral gill arch muscles are typical (see page 25 *et seq.*).

Campylomormyrus elephas (Blgr.)

(Text-fig. 21)

Previously placed in the genus *Gnathonemus*, this species has, on osteological grounds, been reclassified, with others, in the genus *Campylomormyrus* (see Taverne, 1968).

The snout of *C. elephas* is greatly elongate, is tubular and strongly decurved; the tip lies well below the ventral head profile. The mouth is small and, relative to the snout, terminal. Because of the snout's decurvature the mouth opening is directed ventrally. The lower lip is continuous with a short, root-like mental barbel.

Posterior intermandibularis (text-fig. 15A and B): is a complex muscle, paired posteriorly, single anteriorly. The single portion extends from about the level of the quadrate-articular joint to the tip of the mental cartilage on which it is inserted. At no point along its length does this part of the muscle insert onto the dentary or articular.

The paired part is subdivided and has, on each side, several sites of origin. A little behind the point where the two halves of the muscle unite, each is divisible into more or less readily distinguishable dorsally and posterodorsally directed branches (text-fig. 15A). The area between these divisions is, however, traversed by a few interconnecting fibres. The dorsal branch is attached to the dentary and the articular while the posterodorsal branch is attached only to the interoperculum. The points of attachment should be considered as the sites of origin for the muscle as a whole.

Near the insertion of the posterodorsal branch (on the interoperculum) it is joined by a third division which originates, aponeurotically, over the hyohyoideus. This third branch, compared with the hinder part of the posterior intermandibularis in

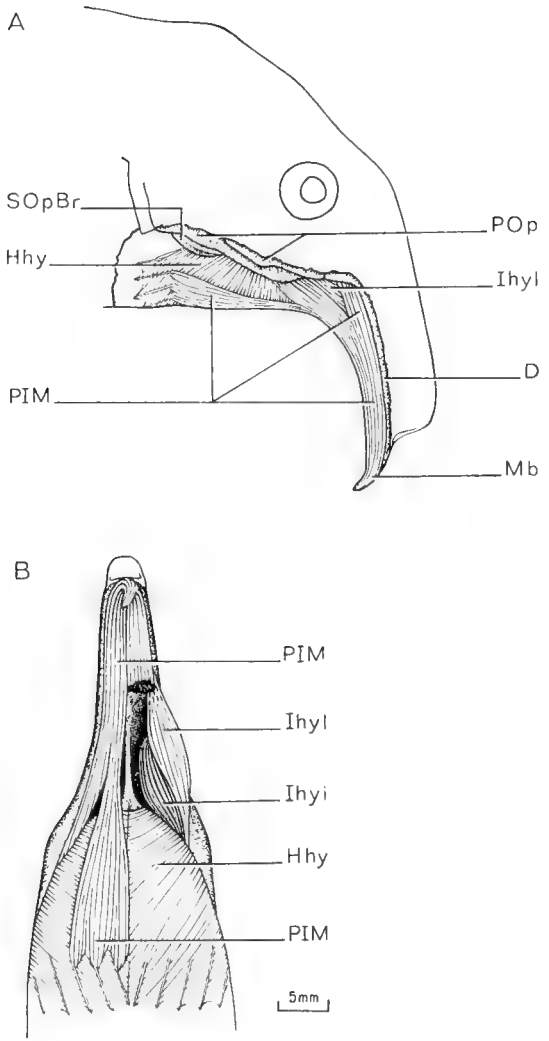


FIG. 15. *Campylomormyrus elephas*: A. Ventral hyoid muscles in lateral view after removal of the skin. B. The same, in ventral view, with the posterior three quarters of the left half of the posterior intermandibularis removed, and the left lateral division of the interhyoideus displaced laterally.

other mormyrids, is rather narrow and does not join its counterpart, although the two approach one another closely in the midline (see text-fig. 15A).

The *anterior intermandibularis* is, apparently, absent.

The *interhyoideus* (text-fig. 15B) like that of *Gnathonemus*, is incompletely subdivided (see page 33).

The *hyohyoideus* conforms with the typical pattern for mormyrids.

The *sternohyoideus* originates, about equally, from the cleithrum and the hypaxial body muscles. It inserts onto the urohyal and has close connections with the second basibranchial and other ventral elements of the first two gill arches. The processes from the second hypobranchials are embedded proximally; distally each lies superficially on, but attached to the sternohyoid flank.

The *ventral gill arch muscles* are typical (see page 25); the muscle linking the fourth and fifth ceratobranchials is present.

Petrocephalus bane (Lacép.)

(Text-fig. 2J)

The snout is short and broad, the mouth broad and subterminal, and lies almost immediately below the eye.

The text-figures for *P. catostoma* are, in general, applicable to this species as well.

Posterior intermandibularis. The two halves of this muscle are narrowly separated medially by a fine aponeurosis. The muscle originates from the first two branchiostegal rays and from above the hyohyoideus. It inserts, tendinously, along the entire ventral margin of the short lower jaw from symphysis to articular-quadrate joint. The uppermost fibres of this muscle separate easily from the ventral fibres, and in one specimen there appears to be some exchange of fibres between the posterior intermandibularis and the overlying interhyoideus muscle (see below). Close contact between these muscles is enhanced by the complete absence of an *anterior intermandibularis*.

Petrocephalus bane, unlike the species described before, has only one *interhyoideus* present on each side. The muscle, despite its great relative depth has a narrow origin on the dorsal part of the anterior face of the ceratohyal. In contrast, it has a deep and extensive insertion on the inner aspect of the dentary and articular, linearly from a point near the symphysis almost to the joint with the quadrate, and vertically from dorsal to ventral margins of these bones.

The *hyohyoideus* is well-developed and of the usual form, except that only a very small part is inserted onto the urohyal.

The *sternohyoideus* originates about equally on the cleithrum and from the hypaxial body muscles.

The *ventral gill arch muscles* are typical, with a small interceratobranchial muscle between the fourth and fifth arches (see page 25 *et seq.*).

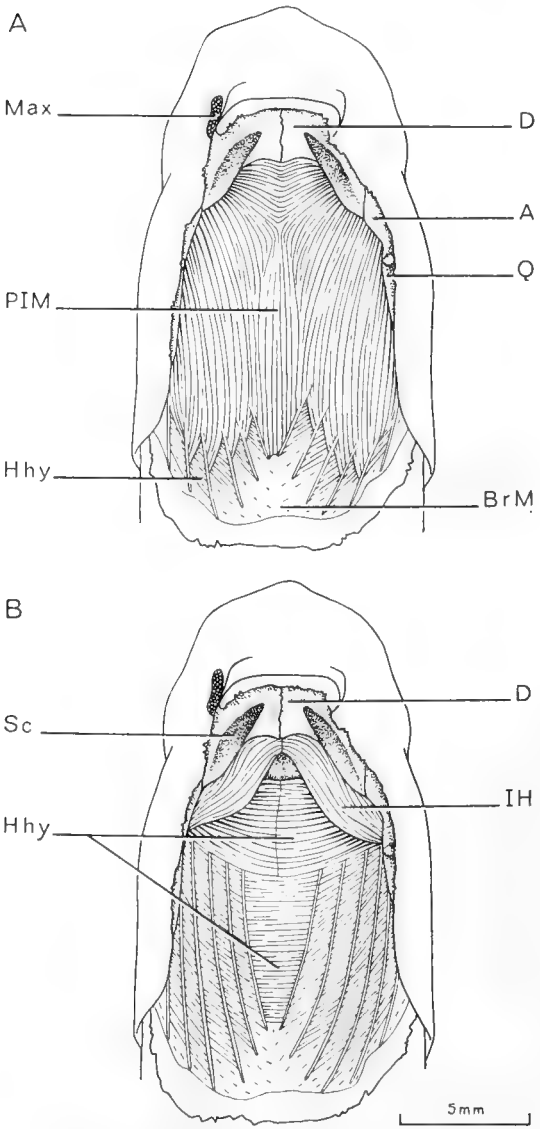


FIG. 16. *Petrocephalus catostoma*: ventral hyoid muscles. A. After removal of the skin. B. After removal of the posterior intermandibularis muscle.

Petrocephalus catostoma (Günther)

In its superficial morphology this species closely resembles *P. bane*; the myology is likewise very similar.

The *posterior intermandibularis* (text-fig. 16A) of *P. catostoma* has a more extensive origin over the hyohyoideus, and the tendinous part of the insertion is wider in this species. Some anterior fibres are almost transversely arranged (text-fig. 16A), thus contrasting with the obliquely orientated fibres posteriorly. Since no distinct *anterior intermandibularis* can be located in this species either, it is tempting to consider these transverse fibres as remnants of an anterior muscle now fused with the posterior part.

As in *P. bane*, only one interhyoideus (text-fig. 16B) is present on each side. These muscles are completely free from the underlying intermandibularis.

In all other respects the musculature of the two species can be considered identical, and typical of the family.

Isichthys henryi Gill

(Text-fig. 2K)

The broad snout of this species is relatively short and is not at all decurved. The mouth is terminal, horizontal and rather broad.

The *posterior intermandibularis* (text-fig. 17) of *I. henryi* shows very considerable reduction when compared with that muscle in all the species described above. The

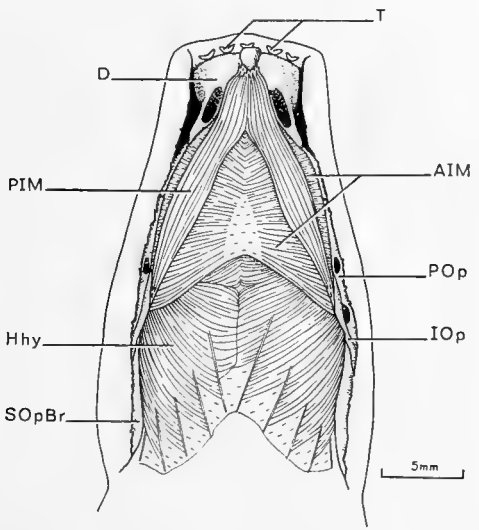


FIG. 17. *Isichthys henryi*: ventral hyoid muscles, after removal of the skin.

muscle is reduced to a narrow V-shaped band of fibres with the apex directed anteriorly; its origin is entirely from the interoperculum, and its tendinous insertion is onto the small mandibular cartilage lying above the interdentary symphysis.

Overlying the narrow posterior intermandibularis is the broad *anterior intermandibularis* (text-fig. 17) which extends across the lower jaw from the level of the posterior interopercular margin to immediately behind the interdentary symphysis. The muscle has a largely musculose insertion onto the ventral margins of the dentary and articular; its fibres are separated medially by a posteriorly broad but anteriorly narrow aponeurosis. Over the anterior quarter of the muscle the fibres are arranged almost transversely, but elsewhere they run obliquely forward.

The *hyohyoideus* (text-fig. 17) shows typical hypertrophy, and there are distinct lateral and medial *interhyoideus* muscles on each side.

The *sternohyoideus* originates about equally from the cleithrum and, aponeurotically, from the hypaxial body musculature. As usual, the sternohyoid is closely associated with the ventral elements of the first two gill arches. The ventral processes of the second hypobranchials lie superficial to the lateral surface of the sternohyoid, but are closely bound to it by connective tissue.

The *ventral gill arch musculature* conforms to the typical pattern (see page 25); the small muscle between the fourth and fifth ceratobranchials is not clearly differentiated and seems to be a slip from the *anterior transversus*. The *posterior transversus* is a narrow muscle but is otherwise typical.

Mormyrops anguilloides (Linn.)

(Text-fig. 2L)

The snout is relatively short in *M. anguilloides*, and is not decurved. The mouth is wide and terminal.

A specimen of the closely related *M. deliciosus* (Leach) was also dissected and its musculature found to be identical with that of *M. anguilloides*.

Posterior intermandibularis (text-fig. 18A). The muscle thought to be a posterior intermandibularis (see below) is a largely tendinous sheet within which lies a narrow band of transverse fibres arranged on either side of a median aponeurosis. Posteriorly, a short, upwardly directed slip of muscle runs to each interopercle; there is also a broader posterior extension of the muscular part which ends, aponeurotically, above the hyohyoideus (text-fig. 18A). Fibres in this part of the muscle are longitudinally orientated. The attachments to the interoperculum and the aponeurotic connection over the hyohyoideus should, presumably, be considered as the origins of the muscle; its insertion is directly onto the dentary near and on the symphysis (there being no mental cartilage in this species). The lateral and tendinous part of the muscle is attached to the interopercula, preopercula, the articulars and the dentaries.

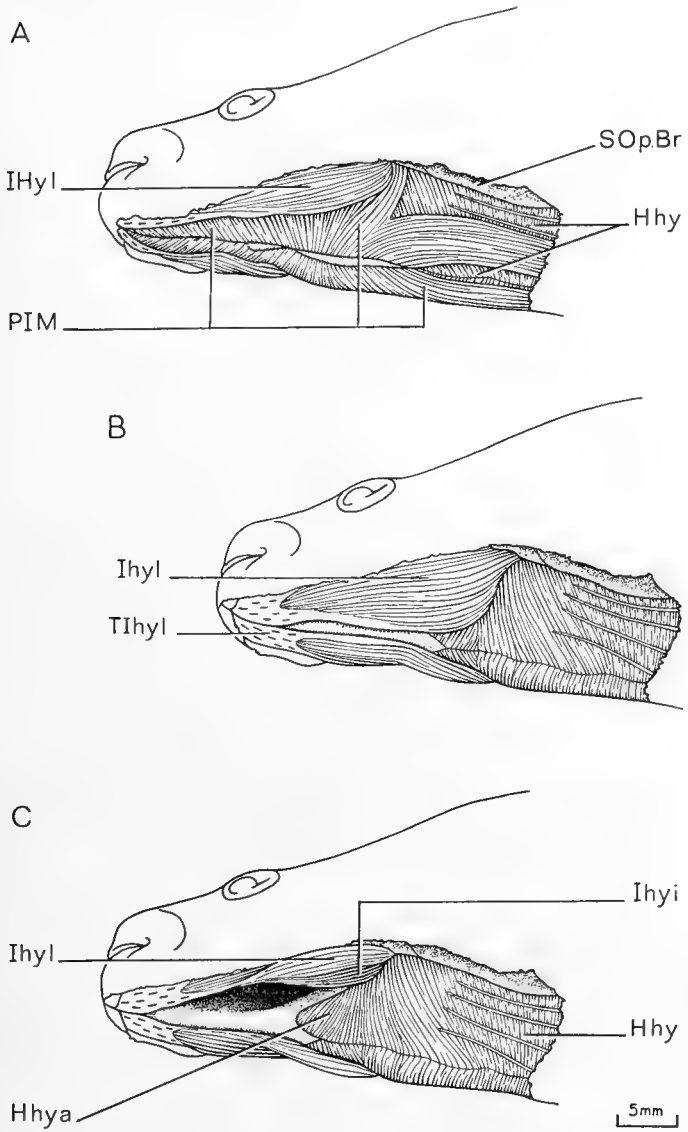


FIG. 18. *Mormyrops anguilloides*: oblique ventro-lateral view of the ventral hyoid muscles. A. After removal of skin. B. After removal of posterior intermandibularis muscle C. As in B but with lateral division of left interhyoideus reflected to show the inner division of that muscle.

No discrete *anterior intermandibularis* is present. The possibility of this muscle having fused with the posterior division cannot be overruled because the muscle thought to be the posterior intermandibularis is fairly clearly demarcated into an anterior part with transverse fibres, and a posterior sector with longitudinal fibres (see above). If the posterior and anterior intermandibulares are fused, then *Mormyrops* presents a rare condition among the mormyrids (but see also *Petrocephalus catostoma*).

The interhyoideus in *Mormyrops* also exhibits certain peculiarities (text-fig. 18B, C). As is usual, the lateral muscle of each pair is the larger. It originated dorsally on the anterior face of the ceratohyal, but it has two insertions, one directly onto the inner and ventral aspects of the dentary and articular, the other, tendinously, onto the anteroventral face of the dentary immediately lateral to the symphysis.

The smaller median muscle also originates on the anterior face of the ceratohyal but it inserts, aponeurotically, onto the median aspect of the lateral muscle. In other words, it has no direct attachment to the lower jaw. Indeed, the separation between the two muscles is very slight even near their origins and there is an exchange of fibres between them (a condition reminiscent of that in *Gnathonemus* and *Campylomormyrus* [see pages 33 and 35 respectively]).

The *hyohyoideus* (text-fig. 18) shows typical hypertrophy and relationships with other structures (see page 25).

Most of the *sternohyoideus* originates as an extension of the ventral body musculature; only a small part stems from the cleithrum. The processes from the second hypobranchials are fairly deeply embedded in muscle.

The *ventral gill arch muscles* are typical (see page 25), but the small muscle between the fourth and fifth ceratobranchials appears to be missing, and the slip from the first obliquus is greatly reduced in size.

The *pharyngocleithrales* are moderately well-developed, especially the external division.

Hyperopisus bebe (Lacép.)

(Text-fig. 2M)

The snout is relatively short and not decurved, the mouth moderately broad, terminal in position and horizontally directed.

Hyperopisus bebe is unique among mormyrids in having greatly enlarged and molariform teeth on the parasphenoid and apposing basibranchial tooth plate. Not only are the teeth enlarged, but they occupy a much broader area of attachment in both places than is usual among species with small conical teeth (see figs. in Taverne, 1968).

The *posterior intermandibularis* (text-fig. 19A) shows a degree of reduction comparable with that in *Isichthys*. From the interoperculum of each side a moderately

developed, strap-like muscle extends forward to insert on the small mental cartilage. Dorsally, the muscle has no contact with the ventral margin of the lower jaw. Between the arms of the strap-like muscle there is a broad tendinous sheet of tissue extending back to about the level of the posterior interopercular margin. Here it becomes continuous with the tendinous part of the overlying anterior intermandibularis. The margin of the tendon passes insensibly into a number of weak muscle-fibre bundles which, in turn have an aponeurotic connection with the hyohyoideus (see text-fig. 19A).

Immediately above the posterior intermandibularis is the well-defined and thick *anterior intermandibularis*. Except for a short distance posteriorly there is no median aponeurosis in this muscle, whose fibres extend from side to side of the lower jaw (text-fig. 19B). Insertion is onto the ventral margins of the dentary, articular, preoperculum and interoperculum, and, anteriorly, onto the mental cartilage. The anterior intermandibularis extends from the level of the vertical preopercular arm to a little behind the interdentary symphysis.

The *interhyoideus* muscles have a characteristic and complex form in *Hyperopisus* (text-fig. 19C–D). The ventro-lateral muscle of each pair is the smaller and is largely tendinous (see text-fig. 19C–D). It originates on the epihyal (with a very small part from the head of the fourth branchiostegal ray), and runs straight forward to insert on a low ventral process of the dentary.

The inner and dorsal muscle is divided, from near its origin, into two elements, one directed horizontally, the other (the innermost) running laterally and anteriorly (text-fig. 19C–D). The medial subdivision is the smaller of the two. It arises from some of the dorsal and external fibres of the lateral subdivision near the upper part of its origin. From a narrow beginning, the medial subdivision fans out so that it comes to extend along the ventral margin of the urohyal (anterior, that is, to the insertion of the hyohyoideus). The left and right medial subdivisions meet in a fairly narrow aponeurosis over the urohyal; some fibres from the underlying anterior intermandibularis also are attached to this tendinous tissue. Anteriorly, the aponeurosis is extended as a short tendon which inserts onto the dentary immediately below the symphysis.

The lateral subdivision of the inner interhyoideus has a broad origin from almost the entire anterior face of the ceratohyal. Its fibres run outwards and forwards, crossing above those of the outer division. The muscle inserts, either directly or through a narrow tendinous margin, onto the inner aspect of the quadrate, articular, and anteriorly, the dentary (text-fig. 19C–D).

The *hyohyoideus* (text-fig. 19C–D), although well-developed, gives the impression of being relatively less massive in this species. The anterior section is not as thick as in the other species described, and the interbranchiostegal portions are also weaker. As usual, the hyohyoideus inserts on the interoperculum, ceratohyal and urohyal, the latter insertion being relatively more extensive than in most of the other mormyrids examined.

The *sternohyoideus* is a short, deep muscle whose origin is entirely from the dorsal face of the cleithrum. The processes from the second hypobranchials curve out-

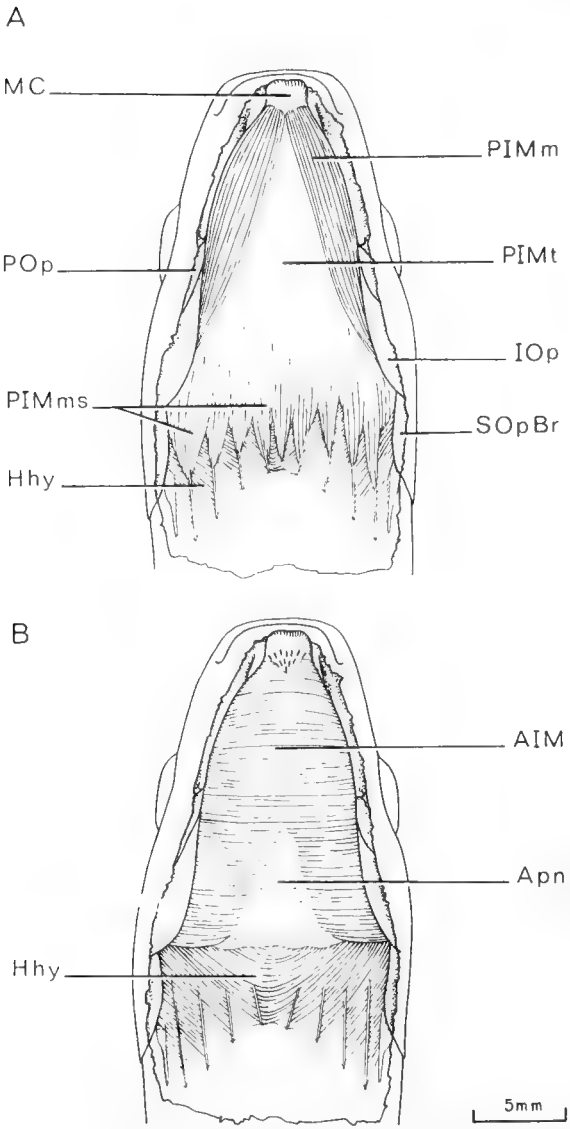
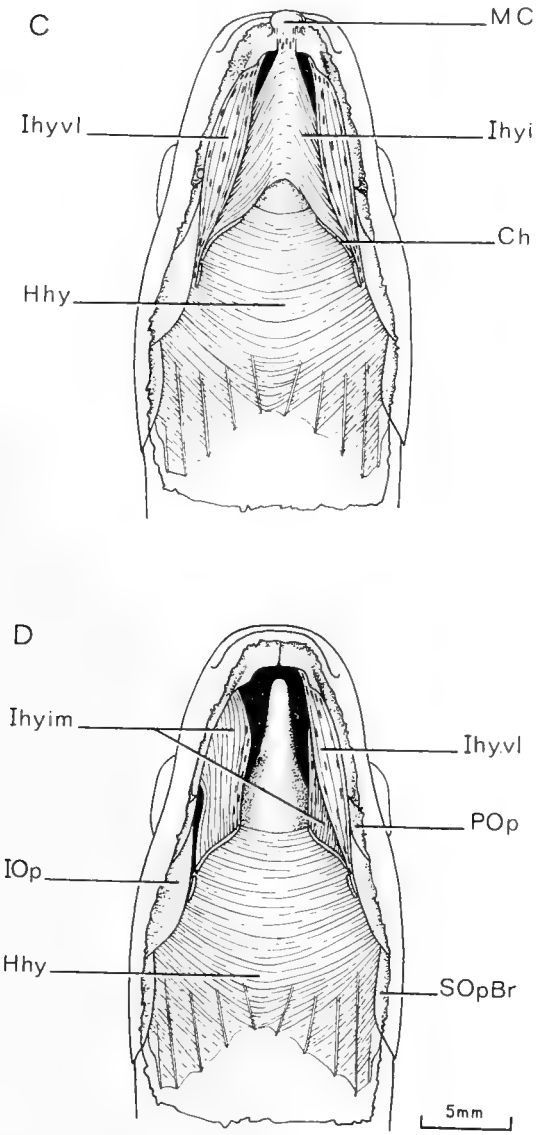


FIG. 19. *Hyperopisus bebe*: ventral hyoid muscles. A. After removal of skin. B. After removal of posterior intermandibularis muscle and tendon complex. C. After removal of anterior intermandibularis muscle. D. Right ventro-lateral division of the interhyoideus muscle removed to show underlying innermost division of this muscle complex. Entire inner (medial) division of this complex also removed.


C
MC
Ihyvl
Ihyi
Ch
Hhy
D
Ihyim
Ihyvl
POp
IOp
Hhy
SOpBr
5mm

wards and slightly backwards so as to lie almost horizontally; each lies superficial to the sternohyoid but is closely bound to that muscle.

The *ventral gill arch musculature* is like that of *Mormyrus* (see page 25), except that there is no muscle linking the fourth and fifth ceratobranchials. The external *pharyngocleithralis* has a short tendinous section at about the middle of its visible length, and the entire external division is virtually tendinous.

Family **GYMNARCHIDAE**

Gymnarchus niloticus Cuvier

(Text-fig. 2N)

The snout in *Gymnarchus niloticus* is relatively elongate, moderately broad and is not decurved. The terminal mouth is horizontally placed and its cleft extends much further posteriorly than in any mormyrid species. *Gymnarchus* is also unusual in having no teeth on the parasphenoid, and in lacking basibranchial tooth plates (see Nelson, 1968 and Taverne, 1970).

Holmquist (1911) has given a fairly detailed account of certain muscles; his description and figures were later used by Edgeworth (1935). Neither author was able to carry out comparative studies on other mormyroids and it is thus understandable how they came to emphasize the apparent similarities between *Gymnarchus* and *Albula*, in particular the hyperdevelopment of the transverse intermandibularis muscle.

Although these similarities do exist, and although *Gymnarchus* departs from the typical mormyrid condition, the similarities between it and *Albula* are less than those shared with the Mormyridae. In particular, one may note the shared specializations in the ventral gill arch musculature and the sternohyoideus.

The *hyoid musculature* (text-fig. 20). Immediately below the skin, and closely adherent to it, there is a broad, generally thick sheet of muscle which thins out posteriorly. It is attached to the operculum, sub- and interopercula, the preoperculum, dentary and articular. Anteriorly, this muscle inserts around the ventral margin of the mandibular arcade; posteriorly it extends to the level of the branchial opening (text-fig. 20). Throughout its length the fibres of the muscle are transversely arranged and extend from side to side without any indication of a median aponeurosis. Innervation is from a branch of the mandibular V nerve.

Holmquist (*op. cit.*) identifies this muscle as an intermandibularis; from the transverse arrangement of its fibres (text-fig. 20) it would seem to be homologous with the *anterior intermandibularis* of mormyrids. Since there is no trace of any muscle ventral to this sheet, and because there are no indications of longitudinal fibres in the sheet, one must conclude that a posterior intermandibularis is absent.

Immediately above the intermandibularis is a pair of muscles that insert, anteriorly, on the inner aspect of the dentary on either side of the symphysis (text-

fig. 20). Neither muscle meets the other at any point, although they are closely aligned anteriorly. The muscles originate in part from the epi- and ceratohyal, and in part from the first branchiostegal ray. In large individuals each muscle is incompletely divided, horizontally, so as to virtually form a small dorsal and larger ventral muscle (text-fig. 20). The ventral subdivision is that described above; the dorsal part originates on the epihyal and inserts on the inner face of the dentary about halfway along its length. The smallest fish examined (14·0 cm standard length) has no division, or even incipient division, in the muscle; consequently the single muscle on each side appears to have a double insertion, one anteriorly and the other laterally at about the middle of the dentary.

These muscles (or muscle) correspond, in most details, to the *interhyoideus* of mormyrids, and are identified as such in *Gymnarchus*.

One difference in the interhyoid of *Gymnarchus* is the considerable proportion of muscle originating from the first branchiostegal ray (text-fig. 20). In mormyrids the interhyoid originates exclusively from the hyoid bar, and there is complete separation between the interhyoid and the hyohyoideus. The situation in *Gymnarchus* is very different. In fact, the muscle described above could well be a combined inter- and hyohyoideus. In *Gymnarchus* the only clearly recognizable *hyohyoideus* is the superior or interbranchiostegal ray portion (text-fig. 20); here it is represented by a few, well-spaced oblique fibres running between the branchiostegal rays. No distinct inferior hyohyoid can be recognized. Indeed, those fibres, which, topo-

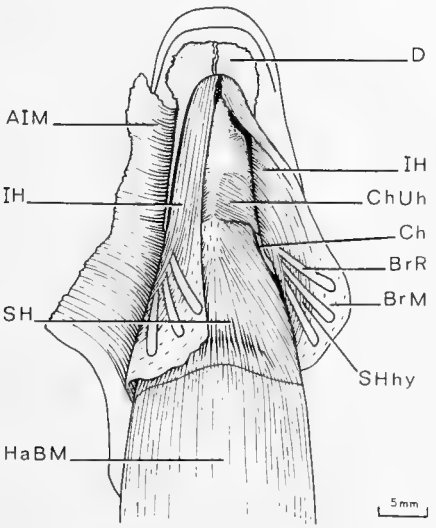


FIG. 20. *Gymnarchus niloticus*: ventral hyoid musculature. Anterior intermandibularis cut and reflected to the right; left interhyoideus reflected to the left.

graphically, would form the inferior hyohyoid merge with the fibres forming the body of the muscle I have identified as the interhyoideus. Thus, the situation in *Gymnarchus* has all the appearance of a secondary return to the primitive condition in which the constrictor hyoideus ventralis has not split into inter- and hyohyoid portions. That the condition is not strictly a primitive one is indicated by the separate left and right inter- cum-hyohyoideus muscles.

The poorly developed hyohyoideus of *Gymnarchus* contrasts markedly with the hypertrophy of that muscle in all mormyrids. *Gymnarchus* also differs in having the branchiostegal rays (and their associated musculature) free from the ventral body muscles. Nevertheless, the branchiostegal membrane (*i.e.* the interray muscles and tendons) still does not provide a ventrolateral floor to the branchial cavity. This is formed by a membranous sheet which runs, on each side, from the inner face of the corresponding ceratohyal to the upper part of the sternohyoid muscle. In effect, each branchiostegal membrane constitutes a lateral half pouch (opening medially but blind anteriorly) over the sternohyoid and hypaxial muscles. The intermandibularis muscle covers these pouches and their medial openings. This greater pouch is open posteriorly across the breadth of the body.

Identifying the hyoid muscles of *Gymnarchus* is further complicated by the presence of a pair of small muscles that lie immediately anterior to the sternohyoid

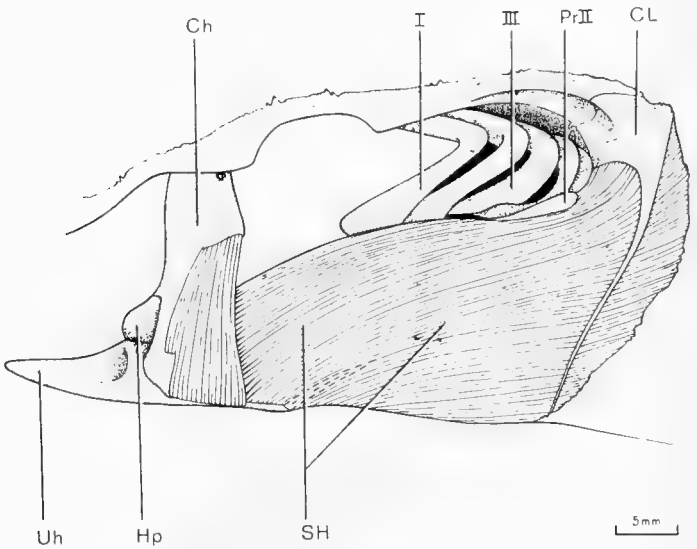


FIG. 21. *Gymnarchus niloticus*: Sternohyoid and ceratohyal-urohyal muscles in left lateral view; semi-schematic.

insertion (text-figs 20 & 21). Each muscle has its fibres arranged almost vertically, and is attached to the ventral margin of the ceratohyal above and to the urohyal below. It seems likely that these are the muscles which Holmquist (*op. cit.*) showed in his figure and which he tentatively identified as branchio-mandibulares (labelled:? genio-branchialis in Edgeworth's [1935] reproduction of Holmquist's figure). However, Holmquist does clearly state that the fibres run longitudinally.

Holmquist (*op. cit.*) commented that he had not seen such a muscle in any other teleosts, and neither have later workers described similar muscular arrangement.

Holmquist's and Edgeworth's identification of this muscle are tentative, but I have difficulty in understanding why they considered it to be a branchiomandibularis or geniobranchialis. Such a muscle is not found in teleosts, and morphologically it is one connecting the lower jaw with the hyobranchial skeleton. Be that as it may, the identification of the muscle pair still poses several questions. That each is attached to both the ceratobranchial and the urohyal suggests one of three things: that the muscle could be a subdivision of the interhyoideus (see *Hyperopisus*, p. 41), could be part of the sternohyoideus (see *Arapaima*, p. 15 and *Papyrocranus*, p. 20), or could be a separated segment of the hyohyoideus. Without ontogenetic studies it seems unlikely that an answer can be provided.

The *sternohyoideus* (text-figs 20 & 21) is a large muscle originating almost entirely from the dorsal face of the cleithrum, but with a few ventral fibres contributed by the hypaxial body musculature. Each ventral process from the second hypobranchial is very large, stout, and orientated so as to lie horizontally along and within the upper border of the sternohyoid (see fig. 21). Because the cleithrum is almost vertical in position and without a forwardly directed arm, the ventral processes form the ventral margins to the branchial chamber; in mormyrids the dorsal surface of the horizontal arm of each cleithrum forms the margin. The great size and peculiar orientation of the ventral processes in *Gymnarchus* appears to be unique within the Mormyriformes.

Ventral gill arch muscles in *Gymnarchus* conform to the usual mormyrid pattern but show several modifications doubtless associated with the reduced branchial skeleton in this genus (Taverne, 1970; Nelson, 1968).

The *obliquus* of the first gill arch is a stout muscle with a double insertion onto the anterior and posteroventral margins of the ceratobranchial; its origin covers most of the ventral surface of the hypobranchial. The second obliquus is a much smaller muscle. There is no obliquus muscle on the third arch, whose ceratobranchial is closely associated with the *rectus communis* muscle linking the fourth ceratobranchial with the base of the ventral process from the second hypobranchial.

The *pharyngocleithrales* are relatively stout muscles which can only be seen after deep dissection because they originate on the medial side of the sternohyoid (*cf.* mormyrids where the origin is lateral to that muscle). The near vertical cleithrum also effects the alignment of these muscles which thus originate behind the fifth ceratobranchial.

The internal muscle of each pair is the larger and longer; it runs obliquely forward and upwards to insert on the ventral tip of the ceratobranchial. The external

muscle is flatter and thinner, and runs almost vertically upwards to insert on the ventral face of the bone near its median edge and posterior border.

The *transversus* of the fourth arch is a fairly broad muscle linking the ventral tips of the ceratobranchials. The transversus of the fifth arch, however, joins the ceratobranchials near their posterior (*i.e.* upper) borders, and is in close contact with the external pharyngocleithrales near their points of insertion. This arrangement contrasts with that in the Mormyridae, where the fifth transversus runs forwards and medially as a V-shaped muscle to attach to the cartilaginous basibranchial plate between the fourth and fifth arches.

SUMMARY AND DISCUSSION

For the purpose of this discussion, the term ventral hyoid musculature includes the anterior and posterior intermandibulares, and the interhyoideus muscle (with its subdivisions), either as separate entities or with some elements partly fused to form a protractor hyoideus (see Introduction, page 4). My use of the term protractor hyoideus differs somewhat from that employed by Edgeworth (1935, p. 101). This implies neither criticism nor acceptance of Edgeworth's concepts, and is used merely for brevity's sake (but see page 49 below).

Among the Osteoglossomorpha, two principal types of ventral hyoid musculature can be recognized. In one there is a protractor hyoideus (Hiodontidae, Osteoglossidae and Pantodontidae), while in the other the posterior intermandibularis and the interhyoideus muscles are quite separate (Notopteridae and Mormyridae). *Gymnarchus* could, perhaps, be considered as constituting a third type, but I would prefer to consider its pattern as a modified mormyrid type (see below).

The pattern shown by *Hiodon* is the most unspecialized one, and compares closely with that of the holostean *Amia* and such primitive teleosts as *Elops* and *Megalops*. Compared with the protractor hyoideus in these fishes, that of *Hiodon* is a little more specialized because the component muscles show a greater degree of consolidation and unification (see page 9).

Apart from some slight intergeneric variations, the protractor hyoideus in the Osteoglossidae and Pantodontidae presents a uniform picture. Compared with *Hiodon*, consolidation of component muscles is carried even further. The compound muscle is, indeed, like that occurring in species of several euteleostean groups (*e.g. Salmo, Abramis* and *Peristedion*: see Edgeworth, 1935). Edgeworth (*op. cit.*), based on Holmquist's (1911) studies, interprets the ventral hyoid muscles in *Osteoglossum* as having the posterior intermandibularis " . . . attached by intersection to the inner part of the Interhyoideus, so that externally there is an Interhyoideus which reaches the jaws and internally a Protractor hyoidei". This description certainly fits the condition found in *Pantodon* (see page 16), but in the other osteoglossoid genera (including *Osteoglossum*) I can find no such clear-cut division into ventrally placed posterior intermandibularis and dorsal interhyoideus (see page 12). The impression gained is one of greater fusion between the two muscles (if indeed

they are arranged in a dorsoventral series). From adult anatomy it seems that an anteroposterior fusion is just as probable, the forward section being derived from the posterior intermandibularis muscle, the hinder part from the interhyoideus (see page 12). In other words, a condition fulfilling Edgeworth's definition of " . . . a fully developed Protractor hyoidei . . . —a longitudinal muscle the anterior part of which is formed by the Intermandibularis posterior and the posterior part of the Interhyoideus".[1]

The unconsolidated ventral hyoid muscles in notopterid and mormyrid fishes represent a different line of specialization, and one apparently otherwise seen only in siluroid ostariophysans (see pages 18 & 25).

In both notopterids and mormyrids the most superficial muscle is the posterior intermandibularis. The Gymnarchidae have lost the posterior intermandibularis, and thus the superficial muscle is probably an expanded anterior intermandibularis (see page 44). In all three families the interhyoideus component is a deep muscle, relatively small in notopterids but enlarged (and generally subdivided) in mormyrids and gymnarchids. There is also a difference in the way in which the interhyoideus inserts. Notopterids have the insertion on the hypohyals, but in the two other families the muscle is attached to the medial face of the lower jaw.

There is little intergeneric variation in the hyoid musculature of notopterids but a considerable amount within the mormyrids, involving all elements, including the anterior intermandibularis muscle.

Recent studies on the anatomy and osteology of mormyrid and gymnarchid fishes all indicate that species of the genus *Petrocephalus* are probably the least specialized (see Nelson [1968] on branchial arches; Taverne [1968, 1969 and 1970] on osteology, and Orts [1967] on visceral and auditory anatomy). *Petrocephalus* is also outstanding for being the only mormyrid in which the interhyoid of each side remains undivided. Of the other ventral muscles in *Petrocephalus*, the posterior intermandibularis is well-developed and expansive, but the anterior intermandibularis is absent (or, possibly, fused with the posterior muscle; see page 37). The anterior intermandibularis is present in other genera with relatively unspecialized cranial characters, for example *Marcusenius* which closely resembles *Petrocephalus* in many respects. Thus, the absence of an intermandibularis in *Petrocephalus* may be a specialization.

Equally, the broad and expansive anterior intermandibularis found in *Mormyrus*, *Hyperopisus*, *Isichthys*, and *Gymnarchus* is probably a derived condition, as would be the lack of this muscle in *Gnathonemus* and *Campylomormyrus*, genera showing great specialization in jaw and snout form. The peculiar condition of the intermandibularis muscle (or muscles) in *Mormyrops* (page 38) is difficult to interpret, and is unlike either the *Mormyrus-Marcusenius* or the *Gnathonemus-Campylomormyrus*

[1]If such definite ontogenetic differences exist in the way a "protractor hyoideus" is formed, then there would be every justification for recognizing the end products by different names.

I am less impressed by the validity of Edgeworth's (*op. cit.*) two subdivisions for those fishes without a fully formed (*sensu* Edgeworth) protractor hyoideus (see Edgeworth, *op. cit.*, pp. 100–101). For instance, the differences described by Edgeworth between *Perca* (his division I) and *Osteoglossum* (division 2) seem to be more a difference of degree than of fundamental organisation.

types. The relatively short anterior intermandibularis of *Marcusenius* and *Cyphomyrus* should probably be taken as the least specialized mormyrid condition. Nevertheless, this type still represents a marked departure from the basic teleostean condition (as in *Hiodon*) or even that in the generality of the euteleosts.

The posterior intermandibularis is, in most mormyrid genera, well-developed and expansive. Although this form represents a derived condition as compared with the presumed basal teleostean type (*e.g. Hiodon* and *Elops*), it should probably be considered the primitive condition for mormyrids. Specialization by reduction of this state is seen in *Mormyrops*, *Isichthys* and *Hyperopisus*. This shared specialization cannot alone be taken to imply any phyletic relationship between these genera, especially since the end-product in *Mormyrops* is unlike that of the other two genera. Different specializations of the posterior intermandibularis are seen in *Gnathonemus* (extension in connection with the hypertrophied mental barbel, see page 32) and *Campylomormyrus* (multiple sites of origin, presumably correlated with extreme snout elongation and decurvature; see page 33).

The complete absence of a posterior intermandibularis in *Gymnarchus* is unique among mormyroid fishes, and is associated with a number of other muscular specializations in the hyoid and branchial systems (see page 44). The hyoid and gill arch musculature in this genus are so specialized that they provide few clear-cut phyletic pointers. About all that can be said regarding the relationships of *Gymnarchus* is that the presence in the skull of lateral ethmoids, paired orbitosphenoids, and a basisphenoid (see Taverne, 1970), together with the relatively unspecialized inner ear (Orts, 1967), all point to derivation from the *Marcusenius–Petrocephalus–Mormyrus* assemblage rather than the *Gnathonemus Isichthys–Mormyrops* group.

The sum of characters, both specialized and generalized in *Gymnarchus* suggest that it was a fairly early departure from the main mormyroid stem. Its retention in a distinct, monotypic family is probably not justified on phyletic grounds; its placement in a subfamily (Gymnarchinae) of the Mormyridae, however, would more accurately reflect its relationships.

The ventral branchial muscles in the Osteoglossomorpha are, on the criteria discussed by Nelson (1967), moderately specialized, being comparable with those of *Polymixia* in his series *Elops-Aulopus–Polymixia–Epinephalus*. The presence of obliqui inferiores in the dorsal branchial musculature of mormyrids and osteoglossids is, according to Nelson (1969), a secondary and advanced feature not present in any member of his *Elops–Epinephalus* series.

In Nelson's argument, the development of a rectus communis (and the degree of its antero-posterior extent) is taken to be indicative of specialization. This muscle in Osteoglossomorpha provides something of a puzzle. It is developed in all members of the superorder except in three of the five osteoglossid genera, namely *Osteoglossum*, *Scleropages*, and *Arapaima*.[1] When present the muscle extends from the fourth arch to the second (attaching to the basibranchial in *Hiodon* but to the hypo-

[1]Hence, because these were the species he examined, Nelson's (1969) observation that a rectus communis is not developed in Osteoglossidae; it is, on the other hand, well-developed in *Heterotis niloticus* and *Pantodon buchholzi*.

branchial in all others). In terms of its volume, the muscle is largest in *Hiodon* although its anterior third is entirely tendinous.

Apart from the large rectus communis, the ventral branchial muscles in *Hiodon* show no outstanding characters. As in the notopterids (except *Xenomystus*) and osteoglossids, *Hiodon* has a rectus muscle between the third ceratobranchial and the second hypobranchial, and the well-developed pharyngocleithrales originate medial to the sternohyoideus.

An interesting feature of the notopterids is the way in which the heads of the ventral obliqui muscles on the first two arches attach to both the basibranchials and hypobranchials. The same muscles in mormyrids also have a complex origin, the first attaching to the second hypobranchial as well as to the first, and the second obliquus extending below the hypobranchial of that arch to reach the second basibranchial.

No rectus muscle is developed in mormyrids, but in one species (*Cyphomyrus discorhynchus*) a stout muscle links the ventral ends of the second and third ceratobranchials. Another peculiar muscle, present in most mormyrids (but not in *Mormyrops*, *Hyperopisus* or *Gymnarchus*, and weak in *Isichthys*) extends between the ventral ends of the fourth and fifth ceratobranchials (see page 26). This muscle could be a segment of the anterior transversus muscle. The posterior transversus in all mormyrids except *Gymnarchus* (page 48) is V-shaped with its apex attached to the cartilaginous fourth basibranchial.

The mormyrid pharyngocleithrales are, in general, weak and often tendinous muscles with a deep insertion onto the fifth ceratobranchial, and an origin lateral to the sternohyoideus. *Gymnarchus*, by contrast, conforms with the more usual teleost condition in which the muscles originate lateral to the sternohyoid.

All Osteoglossomorpha, with the exception of *Hiodon*, have a pair of ventrally directed bony processes associated with the ventral end of the second gill arches (see Greenwood *et al.*, 1966 and Nelson, 1968). The processes are closely associated with the sternohyoideus muscle to which they are closely attached or in which they are embedded.

The sternohyoid of *Hiodon* is particularly interesting in this regard, and suggests a way by which the typical osteoglossomorph hypobranchial process might have evolved. In *Hiodon* the main body of the sternohyoid arises, aponeurotically, on the hypaxial body muscles and is ventral to the cleithrum. A small dorsal part of the muscle on each side, however, originates from the cleithrum. Like the ventral part, it inserts of the urohyal, but from its middorsal region a broad slip of near-tendinous muscle runs forwards and inserts on the second basibranchial (fig. 4). The possible significance of this unusually discrete connection is best appreciated when one recalls the ventral processes (or tendon bones) in notopterids. In these fishes the tendon bones articulate with the second basibranchial (and not the hypobranchial as in other osteoglosomorphs), and are closely attached to the dorsal part of the sternohyoid.

The sternohyoid in Notopteridae originates entirely from the cleithrum. Its insertion is unusual since it has tendinous connections both with the hypohyals and

with the ceratohyals; furthermore, the muscle completely surrounds the small urohyal. Since the urohyal has strong ligamentous connections with the basibranchial tooth plate, the sternohyoid has connections, albeit indirect, with that bone as well.

Among the osteoglossids there is some fairly marked variation in sternohyoideus relationships. In all genera, however, the ventral hypobranchial processes are firmly attached to the muscle, which is also closely associated, by connective tissue fascia, with the first hypobranchials. *Arapaima gigas* has a complex sternohyoid (see page 15), subdivided into paired anterodorsal and unpaired ventral portions, the former inserting, through a common tendon, mainly onto the left ceratohyal. It is interesting to note that *Heterotis* (the other member of the subfamily Heterotinae) shows incipient longitudinal division of the sternohyoid anterodorsally (see page 14).

The mormyrid sternohyoideus shows little intergeneric variation, except in the relative proportions of the muscle originating from the cleithrum and from the hypaxial body musculature. All genera have a close association, through membranous fascia, between the muscle and the second basibranchial, and with the ventromedial elements of the first two gill arches (including, of course, the bony processes of the second hypobranchials).

The most outstanding feature of the sternohyoid in *Gymnarchus* is its relationship with the hypertrophied ventral processes. These elongate and robust bones are no longer ventrally directed, but lie horizontally and are embedded in the dorsolateral margin of the muscle (see page 47). The peculiar ceratohyal-urohyal muscle in *Gymnarchus* (see page 46) may be another specialization of the sternohyoid, but the relationships of the two muscles are still far from clear.

The hyohyoideus muscles in all Osteoglossomorpha, except the Mormyridae, conform to the usual teleost pattern.

The Mormyridae are outstanding for the extent to which the hyohyoidei are hypertrophied and so arranged that the "branchiostegal membrane" is virtually immovable (see page 23). The branchiostegal rays are deeply embedded in the thick superior hyohyodei which, in turn, are aponeurotically connected in the midline and are broadly inserted along almost the entire length of the ceratohyals. Because the inner aspect of each "branchiostegal membrane" is attached to the skin covering the ventral body musculature above and medial to them, they completely occlude the ventral opening to the peribranchial chamber. As a result, this opening is greatly reduced in its vertical extent.

Although it is not possible to carry out a reliable functional analysis on the basis of morbid anatomy, the arrangement of the hyohyoideus and sternohyoideus muscles in mormyrids suggests the development of a strong branchial pump. As a means of ingesting small prey, such a device would accord well with the weak jaws, small mouth and "parasphenoid-basihyal bite" of these fishes (see Nelson, 1968).

As with other myological features, the hyohyoideus muscles in *Gymnarchus* depart markedly from the typical mormyrid type (page 46). In this genus, the branchiostegal membrane is free from the overlying skin of the body, and the hyohyoidei are

reduced to a few fibres between the branchiostegal rays. Furthermore, these muscles are continuous with the more dorsally located interhyoidei (see page 45). Since *Gymnarchus* is the only mormyrid lacking parasphenoid teeth and tooth-bearing dermal plates on the basibranchials, it is very likely that the differences in musculature are associated with different feeding methods. That the gape of the mouth is relatively much larger than in the Mormyrinae, may also be significant.

Phyletic relations within the superorder. The ventral gill arch musculature provides little information on this subject. The presence of a rectus communis in some osteoglossoids (see page 18) rather negates the importance of this character in the analysis of gill musculature given by Nelson (1969). Nelson, on the basis of evidence then available noted the presence of this muscle in notopterids and mormyrids, and its absence in osteoglossids.

The hyoid musculature, on the other hand, allows a clear-cut division to be made into fishes with a protractor hyoideus (Osteoglossidae and Pantodontidae), and those in which the posterior intermandibularis and the interhyoideus are distinct muscles (Mormyridae [including *Gymnarchus*] and Notopteridae). The Hiodontidae have a primitive teleostean type of hyoid musculature with respect to which both other types must be considered specialized, albeit along different lines. The osteoglossoid specialization is a common one among teleosts (see Holmquist, 1911; Dietz, 1912; Takahasi, 1925; and Edgeworth, 1935). The notopterid-mormyrid type has otherwise been recorded only in the catfishes (Siluroidei, Ostariophysi).[1] This siluroid type (Holmquist, 1911; Takahasi, *op. cit.*; Munshi, 1960; also personal observations on *Ictalurus nebulosus*, *Parasilurus aristotelensis* and *Bagrus docmac*) is basically like that of the notoperids, but its specializations are of a type not found in the latter fishes (or the mormyrids either) since they are associated with the mandibular barbels. Because, on so many characters, the siluroids are not allied to the osteoglossomorphs, the resemblance in hyoid musculature can only be convergent.

Convergence is an unlikely explanation for the similarities between notopterid and mormyrid musculature; the two groups are related in so many other characters (Greenwood *et al*, 1966; Nelson, 1968 and 1969).

The relationships of the mormyrid fishes within the Osteoglossomorpha are still uncertain. Greenwood *et al.*, (*op. cit.*), give the Mormyridae ordinal status coordinate with all the other osteoglossomorphs (including the Hiodontidae). McAllister (1968) preferred subordinal status, coordinate with the Osteoglossoidei and Notopteroidei, in an order (Mormyriformes) which excluded the Hiodontidae. In a paper reviewing gill arch skeletons within the Osteoglossomorpha, Nelson (1968) pointed out that most authors have given undue emphasis to certain mormyrid characteristics (especially the brain and electric organs). As a result of this stress on differences, the phyletic relations, he thought, are obscured by the hierarchical categories chosen for the Mormyridae. The gill arch studies made by Nelson led him to rearrange the osteoglossomorphs into two suborders in an order, the Osteo-

[1]Munshi's (1960) description of the clupeoid *Hilsa ilisha* gives the impression that, in this species too, the posterior intermandibularis is the principal (and most superficial) hyoid muscle. The interhyoideus, he notes, is absent. I have dissected a specimen of this species and find that, like other clupeoids (see Kirchhoff, 1958) the interhyoideus and posterior intermandibularis are fused to form a protractor hyoideus.

glossiformes. In one suborder (Notopteroidei) he placed those families in which there are either no ventral processes on the second gill arch (Hiodontidae) or the processes are tendon bones articulating with the second basibranchials (Notopteridae). In the other suborder (Mormyroidei) Nelson placed those families in which the processes are bony and fused with the second hypobranchials (Mormyridae, Gymnarchidae, Pantodontidae and Osteoglossidae). Nelson's later studies (1969) on osteoglossomorph infraorbital bones (and some other features) gave no grounds for altering his earlier classification.

I agree with Nelson's (1968) comments on the undue weight given to certain mormyrid characters, but I consider that other evidence indicates closer relationship between the notopterids and mormyrids than between the latter family and the osteoglossids. This evidence (some yet unpublished) is concerned mainly with specializations of the inner ear shared by the notopterids and mormyrids. A specialized inner ear also occurs in the hiodontids (see Greenwood, 1970; and unpublished). All three groups have an otophysic connection (of varying complexity) but none exists in the osteoglossids. Other indicators of relationship between the notopterids and hiodontids are discussed by Nelson (1969, p. 27).

The ventral hyoid musculature of *Hiodon* is too unspecialized to be of value as a phyletic indicator, but the shared specializations of this musculature in mormyrids and notopterids (see above, page 53) seems to reinforce other characters suggesting a relationship between these families. The very different specialization shown by the hyoid muscles of the Osteoglossidae and Pantodontidae implies that these families together represent a distinct lineage.

Until I have completed certain other studies on osteoglossomorph anatomy it would be premature to put forward a revised formal classification of the superorder. However, it seems very likely that any new classification will group (within a single order) the Hiodontidae, Mormyridae and Notopteridae in one category (probably subordinal) and the Osteoglossidae and Pantodontidae in a second, and coordinate category.

ACKNOWLEDGEMENTS

It is with considerable pleasure that I express my gratitude to Dr. Karel Liem of the Field Museum, Chicago, who during his recent visit to London has spent much time discussing various myological problems with me. His great interest in this work has added considerably to the pleasure of its execution, and I have benefited considerably from his experience. To Sharon Chambers go my thanks for the painstaking care she has taken in preparing the text-figures; and to my assistant Gordon Howes, my gratitude for his help in many aspects of the work. Finally, I must thank Miss Elizabeth Todd (Queen Elizabeth College, London University) for making available to me her unpublished observations on the musculature of several clupeoid fishes.

REFERENCES

Allis, E. P. 1897. The cranial muscles and cranial and first spinal nerves in *Amia calva*. *J. Morph.*, **12** : 487–808.

Bishai, R. M. 1967. Cranial muscles of *Mormyrus caschive* (L.): *Anat. Anz.*, **121** : 12–25.

DIETZ, P. A. 1912. *Vergelijkende anatomie van de kaak- en kieuweboogspieren der Teleostei.* Leiden.

EDGEWORTH, F. H. 1928. II. The development of some of the cranial muscles of ganoid fishes. *Phil. Trans. R. Soc. Ser. B*, **217** : 39–89.

EDGEWORTH, F. H. 1935. *The cranial muscles of vertebrates.* Cambridge University Press.

GREENWOOD, P. H. 1963. The swimbladder in African Notopteridae (Pisces) and its bearing on the taxonomy of the family. *Bull. Br. Mus. nat. Hist.* (Zool.), **11** : 377–412.

GREENWOOD, P. H. 1970. On the genus *Lycoptera* and its relationship with the family Hiodontidae (Pisces, Osteoglossomorpha). *Bull. Br. Mus. nat. Hist.* (Zool.), **19** : 257 285.

GREENWOOD, P. H., ROSEN, D. R., WEITZMAN, S. H., & MYERS, G. S. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. *Bull. Am. Mus. nat. Hist.*, **131** : 339–456.

HOLMQUIST, O. 1911. Studien in der von N.N. Trigeminus und Facialis innervierten Muskulatur der Knochenfische. II. Zur vergleichenden Morphologie der M.M. Intermandibularis, Protractor Hyoidei und Hyohyoideus. *Acta Univ. lund.*, n.s., **7** : 47–79.

KIRCHHOFF, H. 1958. Functionell-anatomische Untersuchung des Visceralapparates von *Clupea harengus* L. *Zool. Jb.* (*Anat.*), **76** : 461–540.

LIEM, K. F. 1967. A morphological study of *Luciocephalus pulcher*, with notes on gular elements in other recent teleosts. *J. Morph.*, **121** : 103–133.

MCALLISTER, D. E. 1968. Evolution of branchiostegals and classification of teleostome fishes. *Bull. natn. Mus. Can., Biol. ser.*, **77** no. 221 : 1–239.

MUNSHI, J. D. 1960. The cranial muscles of some freshwater fishes. *Indian J. Zootomy*, **1**, No. 2 : 1–76.

MYERS, G. S. 1960. The mormyrid genera *Hippopotamyrus* and *Cyphomyrus*. *Stanford ichthyol. Bull.*, **7**, no. 4 : 123–125.

NELSON, G. J. 1967. Branchial muscles in some generalised teleostean fishes. *Acta zool., Stockh.*, **48** : 277–288.

NELSON, G. J. 1968. Gill arches of teleostean fishes of the division Osteoglossomorpha *J. Linn. Soc.* (*Zool.*), **47** : 261–277.

NELSON, G. J. 1969. Infraorbital bones and their bearing on the phylogeny and geography of osteoglossomorph fishes. *Am. Mus. Novit.*, No. **2394** : 1–37.

ORTS, S. 1967. Contribution a l'anatomie comparee et a la systematique des mormyroïdes. *Mem. Acad. r. Sci. outremer* (Cl. Sci. nat. med. 8°), N.S., **17** : 1–87.

OSSE, J. W. M. 1969. Functional morphology of the head of the perch (*Perca fluviatilis* L.): an electromyographic study. *Neth. J. Zool.*, **19** (3) : 289–392.

TAKAHASI, N. 1925. On the homology of the cranial muscles of the cypriniform fishes. *J. Morph.*, **40** : 1–109.

TAVERNE, L. 1968. Ostéologie du genre *Gnathonemus* Gill *sensu stricto* [*Gnathonemus petersii* (Gthr.) et espèces voisines] (Pisces Mormyriformes). *Annls. Mus. r. Afr. cent. Ser.* 8°., no. **170** : 1–91.

TAVERNE, L. 1969. Étude ostéologique des genres *Boulengeromyrus* Taverne et Géry, *Genyomyrus* Boulenger, *Petrocephalus* Marcusen (Pisces Mormyriformes). *Annls. Mus. r. Afr. cent. Ser.* 8°., no. **174** : 1–85.

TAVERNE, L. 1970. Note sur l'ostéologie du genre *Gymnarchus* Cuvier (Pisces Mormyriformes). *Bull. acad. r. Belg. Cl. Sci.*, (5), **55** : 63–78.

VETTER, B. 1878. Untersuchungen zur vergleichenden Anatomie der Kiemen-und Kiefermusculatur der Fische. *Jena. Z. Naturw.*, **12** : 431–550.

P. H. GREENWOOD D.Sc.
Department of Zoology
BRITISH MUSEUM (NATURAL HISTORY)
CROMWELL ROAD
LONDON SW7 5BD

A LIST OF SUPPLEMENTS TO THE ZOOLOGICAL SERIES OF THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY)

1. KAY, E. ALISON. Marine Molluscs in the Cuming Collection British Museum (Natural History) described by William Harper Pease. Pp. 96; 14 Plates. 1965. (Out of Print.) £3.75.
2. WHITEHEAD, P. J. P. The Clupeoid Fishes described by Lacepede, Cuvier and Valenciennes. Pp. 180; 11 Plates, 15 Text-figures. 1967. £4.
3. TAYLOR, J. D., KENNEDY, W. J. & HALL, A. The Shell Structure of Mineralogy at the Bivalvia. Introduction. Nuculacea-Trigonacea. Pp. 125; 29 Plates 77 Text-figures. 1969. £4.50.
4. HAYNES, J. R. Cardigan Bay recent Foraminifera (Cruises of the R.V. *Antur*) 1962–1964. (*In press.*)

Printed in England by Staples Printers Limited at their Kettering, Northants, establishment

THE CLUPEOID FISHES DESCRIBED BY FRANCIS DAY

P. K. TALWAR
AND
P. J. P. WHITEHEAD

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 22 No. 2
LONDON : 1971

THE CLUPEOID FISHES DESCRIBED BY FRANCIS DAY

BY
PURNESH KUMAR TALWAR
AND
PETER JAMES PALMER WHITEHEAD

Pp. 57–85; 2 *Plates*, 3 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 22 No. 2
LONDON : 1971

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 22, *No.* 2 *of the Zoological series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation
Bull. Br. Mus. nat. Hist. (Zool.).

©Trustees of the British Museum (Natural History), 1971

TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 31 *December* 1971 *Price* £1.20

THE CLUPEOID FISHES DESCRIBED BY FRANCIS DAY

By P. K. TALWAR & P. J. P. WHITEHEAD

ABSTRACT

FRANCIS DAY described six new clupeoid fishes: *Spratelloides malabaricus, Clupea sindensis, Clupea variegata, Chatoessus modestus, Pellona sladeni* and *Engraulis auratus*. For the first of these the new genus *Dayella* is proposed. Except for the last, all are considered valid. Lectotypes have been chosen from among Day's figured specimens now in the Zoological Survey in Calcutta, except in the case of *E. auratus* for which a British Museum specimen has been chosen. The history of Day's fish collections is briefly outlined; the Calcutta specimens are considered to be the most important, followed by those in Sydney, Vienna, Leiden, Berlin, Florence and Chicago. Apart from some small collections prior to 1870, the British Museum received only the remainders (in 1889).

INTRODUCTION

Francis Day (1829–1889) listed 55 clupeoid species in his *Fishes of India* (1875–8), of which 47 were illustrated, and 46 species are here recognized as valid (Table 1). He described six new species of clupeoid fishes, of which all but one are valid. Day's descriptions and figures are generally good but many diagnostic features essential to modern clupeoid systematics are omitted. Unfortunately, Day did not specify which specimens were used in his original descriptions and a major problem has been to decide in which institution his types are deposited. The full history of Day's collections is complex and will be described elsewhere (Whitehead & Talwar, in preparation) but a brief resumé can be given here.

Day's first ichthyological work, the *Fishes of Malabar* (1865) resulted from his stay in Cochin (1859–64) and from this time stemmed small collections sent to Albert Günther at the British Museum. Day subsequently investigated the fisheries in almost every large river and along most of the coast of India and Burma, making large collections and finally returning to England in 1874 to work on his specimens and write his monumental *Fishes of India* (1875–1888). Unfortunately, a series of bitter quarrels developed between Day and Günther, with the result that Day donated or sold much of his collection to other museums, the British Museum once again receiving material only in the year of Day's death. The following is a summary of the distribution of Day's specimens:

1864–1870	British Museum (15 lots, c. 400 specimens. Day types specified in letters but not in Register)
1865	East India Museum, London (7 species, including *Engraulis auratus*)

1875–1879	Rijksmuseum van Natuurlijke Historie, Leiden (11 lots, c. 500 specimens. Day types claimed in Register)
1876–7	Indian Museum, Calcutta (figured specimens, now in Zoological Survey of India)
1874–1882	Zoologisches Museum, Berlin (many lots, 296 specimens. Day types claimed in Register)
1881–1884	Florence (three lots, 333 specimens, 3 types claimed in Register)
1883	Australian Museum, Sydney (Day collection from International Fisheries Exhibition, London. Day, Bleeker and Blyth types claimed by Whitley, 1958)
1886	Naturhistorisches Museum, Vienna (1000 specimens, 815 species—Day and Bleeker types claimed in Annual Report)
1889	British Museum (c. 5,000 specimens. Day types subsequently recognized); also Leningrad (see p. 85)
1899	Field Museum of Natural History, Chicago (452 Day specimens from British Museum sent in exchange by Boulenger)

The Calcutta specimens include those used by Day in illustrating the *Fishes of India* (specified as such in Registration Book) and these are being listed by Talwar & Chakrapany (in press). We have concluded that, unless a valid lectotype has been chosen already, the figured Calcutta specimens are the most suitable. In his final letter of reconciliation to Günther, Day specified that his type collection of Indian fishes went to Calcutta, his No. 2 to Sydney, No. 3 to Vienna, while Florence, Berlin and Leiden had large numbers of specimens. Thus the British Museum received his remainders, except for types in the pre-1870 lots. This order should be followed in making a lectotype selection.

In the descriptions given here, measurements follow those of previous clupeoid studies (e.g. Whitehead, Boeseman & Wheeler, 1966). Synonomies include references based on Day material or those relevant to the discussion of Day's species. All further synonyms are given by Whitehead (in press). The following abbreviations are used:

AMS	Australian Museum, Sydney
BMNH	British Museum (Natural History), London
FMNH	Field Museum of Natural History, Chicago
MNHN	Muséum National d'Histoire Naturelle, Paris
NHMV	Naturhistorisches Museum, Vienna
RMNH	Rijksmuseum van Natuurlijke Historie, Leiden
ZMB	Zoologisches Museum, Berlin
ZSI	Zoological Survey of India, Calcutta

ACKNOWLEDGEMENTS

For information on the Day collections sent to Leiden, Berlin, Vienna, Florence, Sydney and Chicago, and for the loan of clupeoid specimens from Leiden, Paris and Berlin, we are indebted to Dr M. Boeseman of the Rijksmuseum van Natuurlijke Historie, Dr C. Karrer of the Zoologisches Museum, Dr P. Kähsbauer of the Naturhistorisches Museum, Prof. Leo Pardi of the Museo Zoologico dell'Università,

Dr J. R. Paxton of the Australian Museum, Dr L. P. Woods of the Field Museum of Natural History in Chicago, and Dr M.-L. Bauchot of the Muséum National d'Histoire Naturelle in Paris. The senior author also wishes to thank the Director, Dr A. P. Kapur, and the Superintending Zoologist, Dr A. G. K. Menon, of the Zoological Survey of India, for providing necessary facilities.

Family **CLUPEIDAE**

(Subfamily **CLUPEINAE**)

1. ***Clupea sindensis*** Day, 1878

= ***Sardinella sindensis*** (Day, 1878)

(Plate 1a)

Clupea sindensis Day, 1878, *The Fishes of India*: 638, pl. 163 (2) (Seychelles, Sind, Bombay; figure (life-size) on Karachi specimen, shown 95·5 mm S.L.); *Idem*, 1889, *Fauna British India, Fishes*, **1** : 374 (repeat).

Sardinella sindensis: Chan, 1965, *Jap. J. Ichthyol.*, **13** (1–3) : 11, fig. 21 (key, 44 specimens *ex* Philippines); Whitehead (in press), *Symp. Indian Ocean Adj. Seas. Mar. biol. Ass. India* (key, synopsis, fig.).

MATERIAL.

a. ZSI.2630, a fish 95·5 mm S.L., *ex* Karachi (stated to be basis for Day's figure—LECTOTYPE)
b. ZSI.2614, a fish 90·0 mm S.L., *ex* Karachi (PARALECTOTYPE)
c. AMS.B7642, a fish 118·5 mm S.L. (140·5 mm tot. l.), *ex* Bombay (claimed as type by Whitley, 1958—? PARALECTOTYPE)
d. NHMV (no specimens)
e. RMNH (no specimens)
f. ZMB (no specimens)
g. BMNH.1889.2.1.1919–24, five fishes 77·5–99·5 mm S.L., *ex* Sind (registered as *Clupea venenosa;* one specimen, a skeleton)

Whitley (1958) gave wholesale endorsement to the type designations made in the published list of Day material bought by the Australian Museum in 1883 (Anon., 1885, 1886). This material, which had been shown at the International Fisheries Exhibition in London in 1883, had already been catalogued (Day, 1883) and, although some specimens were marked as the types of Bleeker and Blyth species, none was indicated as a Day type. Day appears to have described the present species on more than one specimen and while the Sydney specimen may be part of the syntypical series, we feel it preferable to designate as lectotype the one specimen that definitely contributed to the original description, *viz.* the Calcutta figured specimen, particularly since Day himself drew the figure.

Day (1878, 1889) tentatively included *Meletta venenosa* Valenciennes in his synonymy, hence the inclusion of the Seychelles in his distribution of the species. The Valenciennes species is *Herklotsichthys punctatus* (Rüppell) (Whitehead, 1967 :

35). The British Museum specimens were not relabelled '*sindensis*' until examined by Regan (1917a); it is unlikely, therefore, that they were used by Day in his description.

Description. Based on the LECTOTYPE, a fish 95·5 mm S.L., *ex* Karachi, ZSI.2630 (basis for pl. 163 (2) of *Fishes of India*) (in parenthesis are given measurements for the Calcutta PARALECTOTYPE, ZSI.2614).

Br. St. 6, D iii 13 (14), P i 14, V i 7, A ii 16, g.r. 36 + 65 (37 + 63), scutes 18 + 14, scales in lateral series 42 (43), transverse 11, pre-dorsal 15 (?).

In percentages of standard length: body depth 25·7 (23·9), head length 26·7 (22·5); snout length 6·5 (6·9), eye diameter 6·3 (6·9), upper jaw length 9·9 (10·6), lower jaw length 12·0 (10·6); pectoral fin length 16·2 (15·0), pelvic fin length 9·9 (8·1), length of anal fin base 15·7 (14·5); pre-dorsal distance 46·1 (43·3), pre-pelvic distance 48·2 (48·9), pre-anal distance 76·4 (77·8).

Body fairly compressed, its width about $2\frac{1}{2}$ times in its depth, the latter more or less equal to head length; belly keeled, scutes partly concealed by scales on either side. Snout equal to or a little greater than eye diameter. Upper jaw reaching to vertical from anterior third of eye; two supra-maxillae, the 1st (anterior) about 5 times as long as deep, the 2nd (posterior) with upper and lower expanded parts similar in shape and size, the whole almost circular; no hypomaxilla; expanded portion of maxilla with faint longitudinal ridges, lower edge of maxilla with fine denticulations posteriorly. Lower jaw profile rising steeply, its depth half its length. Pre-maxillae and vomer edentulous, but fine teeth on either side of dentary symphysis, a median line of conical teeth on tongue and fine teeth on palatines and ecto- and endo-pterygoids.

Gillrakers fine and slender, close-set, the longest about $\frac{1}{2}$ of eye diameter and equal to length of corresponding gill filaments. Pseudobranch present, exposed, with a dozen filaments, its length about equal to eye diameter. Cleithral lobe and bilobed dermal outgrowths from cleithrum well developed. Operculum about twice as high as wide, its lower margin almost horizontal; sub-operculum rectangular. Opercular series and cheek covered by adipose tissue overlying ramifications of sensory canal system. Fronto-parietal region with cuneiform area bearing 8 (9) longitudinal striae; supra-orbitals with about four longitudinal striae.

Dorsal fin origin much nearer to snout than to caudal base; lower part of fin invested in scaly sheath. Pectoral fin tips failing to reach pelvic base by more than one eye diameter, failing to reach vertical from dorsal origin by $1\frac{1}{3}$ eye diameters; no axillary scale but scales above first ray truncated to leave shallow depression for reception of fin. Pelvic fin base below middle of dorsal base, nearer to pectoral base than to anal origin; axillary scale present, almost length of fin. Anal fin slightly nearer to caudal base than to pelvic base; last two rays enlarged, about twice length of antepenultimate ray.

Scales: unexposed portion of scale with one major and four (anterior scales) to six (posterior) minor vertical striae, the former continuous, the latter interrupted at centre of scale; exposed portion of scales with eroded and slightly crenellated posterior border, faint horizontal ridging and small perforations. Pre-dorsal

medial ridge covered by overlapping scale rows on either side. Alar scales absent (probably lost; present in some specimens of BMNH.1889.2.1.1919–24).

Colour: in alcohol, upper ⅓ of body slate-coloured, remainder of flanks silvery-gold. Fins hyaline, but dark spot at base of anterior dorsal rays. Inside face of operculum somewhat dusky.

NOTE. *Sardinella sindensis*, together with *S. gibbosa* (Bleeker), can be separated from other species of *Sardinella* by its slightly higher post-pelvic scute count (15–16, rarely 14 or 17–18; cf. 12–14, rarely 11 or 15—see key in Whitehead, in press). This slight distinction held true in 44 and 159 specimens (respectively) examined by Chan (1965), and also in British Museum material, and it is unfortunate that both lectotype and paralectotype of *S. sindensis* have the lower count of 14. One out of five other Day specimens (BMNH.1889.2.1.1919–24) has 14 post-pelvic scutes. If scute number is diagnostic, then *S. sindensis* can be separated from *S. gibbosa* by its slightly higher range for gillraker numbers (58–72 at 69–122 mm S.L.; cf. 43–63 at 90–150 mm S.L.—figures from Whitehead, in press). Specimens with only 14 post-pelvic scutes can be distinguished from *S. albella* (Valenciennes) and *S. fimbriata* (Valenciennes) by their more slender body (24·5–27·8% of S.L. (Chan, 1965); cf. 32–35 and 28–34% respectively—Whitehead, in press). *Sardinella brachysoma* Bleeker and *S. zunasi* (Bleeker) are also slightly deeper species which are further distinguished by the numerous overlapping or continuous vertical striae on the posterior scales.

(Subfamily **PELLONULINAE**)

DAYELLA gen. nov.

TYPE SPECIES: *Spratelloides malabaricus* Day.

DIAGNOSIS: clupeid fishes with 5–6 branchiostegal rays, a short anal fin (less than 20 rays), small unkeeled pre-pelvic scutes but no post-pelvic scutes, eight pelvic rays, a single (posterior) supra-maxilla, gillrakers present on posterior face of 3rd epibranchial, and posterior frontal fontanelles occluded in adults. A single species known.

2. ***Spratelloides malabaricus*** Day, 1873

= ***Dayella malabarica*** (Day, 1873)

Spratelloides malabaricus Day, 1873, *Proc. zool. Soc. Lond.*: 240 ('Sea, ascending rivers in Malabar, and attaining 3 inches in length'); *Idem*, 1878, *Fishes of India*: 648, pl. 161 (5) ('Western Coasts of India, in rivers and estuaries'; up to 3 inches, figure (? life size) 55·3 mm S.L.); *Idem*, 1889, *Fauna British India, Fishes*, **1** : 400, fig. 124 (repeat).

MATERIAL.

a. ZSI.2246, a fish 51·0 mm S.L., *ex* Malabar (stated to be basis for Day's figure although 4·3 mm shorter—LECTOTYPE)
b. RMNH.2726, a fish 58 mm S.L., *ex* Malabar—PARALECTOTYPE

c. BMNH.1889.2.1.2048, a fish 47·3 mm S.L., *ex* Malabar, stained with alizarin —PARALECTOTYPE
d. Zool. Inst. Leningrad, 8220, a fish 48·3 mm S.L., *ex* Canara —PARALECTOTYPE

The following specimens are *Ehirava fluviatilis*.

e. AMS.B8288, a fish 44·0 mm S.L. (52·0 mm tot. l.), *ex* Malabar (claimed as type by Whitley, 1958)
f. NMV (no specimens)
g. ZMB.10413, three fishes 28·9–35·4 mm S.L., *ex* Malabar.
h. BMNH.1889.2.1.2051, two fishes 40·0–49·1 mm S.L., *ex* Malabar (removed from jar containing BMNH. paralectotype)
i. BMNH.1889.2.1.2050, one fish 53·0 mm S.L., *ex* Malabar (also removed from BMNH paralectotype jar)
j. BMNH.1889.2.1.2052–5, four fishes 46·5–56·2 mm S.L., *ex* Canara (one fish 50·0 mm stained with alizarin; three fishes donated to the Musée Royale de l'Afrique Centrale, Turvuren)
k. FMNH.2379, a fish 49·0 mm S.L., *ex* Canara (numbered 240 and donated by G.A. Boulenger from BMNH collection)

The two species included in the Day material are superficially very similar and hitherto Deraniyagala's *fluviatilis* has been considered a synonym of Day's *malabaricus* (e.g. in Whitehead, 1963). It was not until the single true specimen of *Dayella malabarica* in the British Museum was stained with alizarin and re-examined that the Day material was found to be mixed. Although specimens of *E. fluviatilis* predominate, Day's original description seems to have been based on *D. malabarica* since Day states that the 'dorsal commences slightly before the origin of the ventral'. In *D. malabarica* the dorsal origin is well before the pelvic base, the latter lying below the first *branched* dorsal ray. In *E. fluviatilis* the pelvic base is before, below or only just behind the first *unbranched* dorsal ray. The statement is repeated in Day's second description and in his figure (Day, 1878 : pl. 161) the dorsal origin is clearly well before the pelvic base.

The specimen in Calcutta is slightly smaller than Day's figure but is presumed to have been the model and is here chosen as lectotype of *Spratelloides malabaricus*. The holotype of *Ehirava fluviatilis* Deraniyagala is in London (BMNH.1929.7.1.1); the specimen in the Zoological Survey of India (ZSI.F11043/1), claimed as a paratype by Menon & Yazdani (1963), is from Moratua (Western Province of Ceylon), a locality not mentioned in the original description.

Description. Based on the LECTOTYPE, a fish 51·0 mm S.L., *ex* Malabar, ZSI.2246 (basis for pl. 161 (5) of *Fishes of India*). Figures for the Leiden and British Museum specimens (49·5 and 47·3 mm S.L.—lots b and c above) are given in parenthesis.

Br. St. 6 (5, 5), D iii 11 (11, 11), P i 12 (12, 13), V i 7 (7, 7), A iii 15 (14, 15), C n.r. (n.r., 10 + 9), g.r. 11 + 27 (10 + 24, 10 + 27), scutes ? 0 (4, 1), scales in lateral series 38 (n.r., 36), transverse 9 (n.r., n.r.), vertebrae 40 (BMNH alizarin specimen).

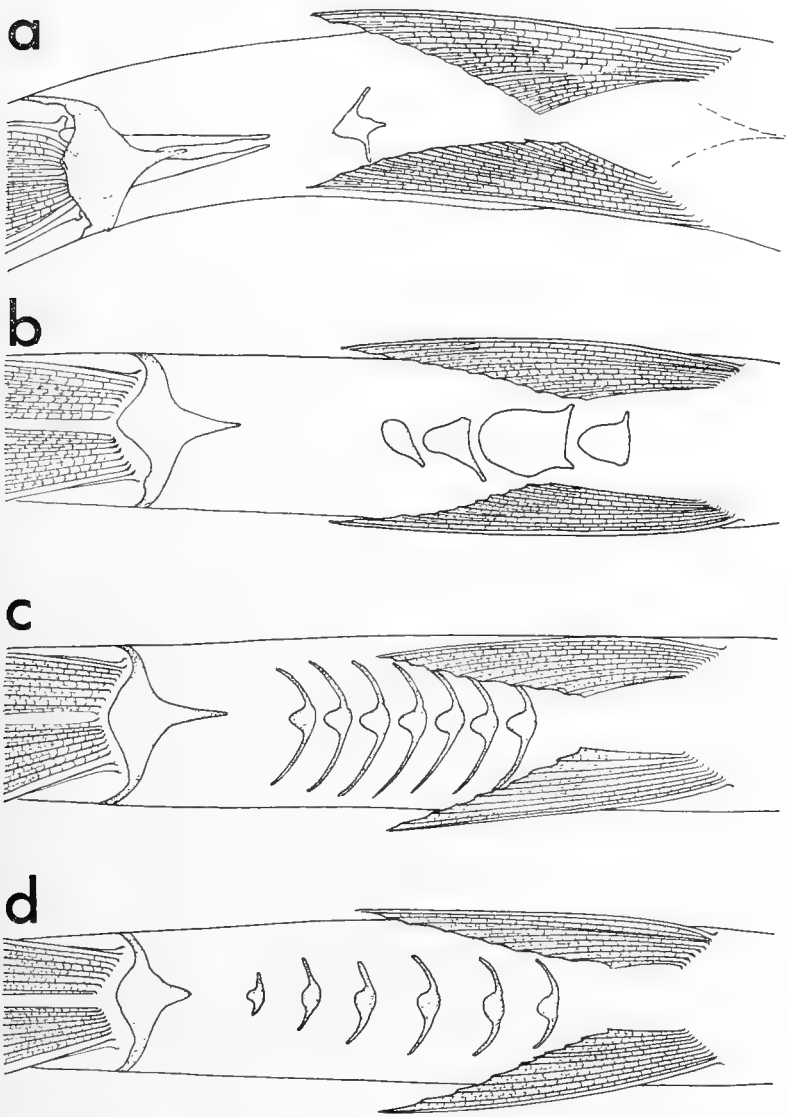


FIG. 1. Pre-pelvic scutes in three Indo-Pacific pellonulines. a. *Dayella malabarica*, 47·3 mm S.L., BMNH.1889.2.1.2048. b. *Dayella malabarica*, 49·5 mm S.L., RMNH.8585. c. *Gilchristella aestuarius*, 52·3 mm S.L., BMNH.1915.7.6.3. d. *Ehirava fluviatilis*, 49·1 mm S.L., BMNH.1889.2.1.2051.

In percentages of standard length: body depth 22·5 (20·0, 20·0), head length 27·7 (24·0, 26·0); snout length 8·3 (7·5, 7·4), eye diameter 8·3 (8·0, 7·8), post-orbital distance 9·9 (8·5, 8·7), length of upper jaw 9·9 (8·7, 9·7), length of lower jaw 14·7 (12·3, 13·1); pectoral fin length 16·7 (17·1, 15·8), pelvic fin length 13·7 (13·3, 14·5), length of anal base 18·6 (15·3, 14·5); pre-dorsal distance 49·0 (47·9, 48·5), pre-pelvic distance 52·9 (50·4, 49·5), pre-anal distance 78·4 (77·3, 75·0).

Body fairly compressed, its width almost 3 times in its depth, the latter a little less than head length; belly rounded, fully scaled but the scales underlain by 4 (Leiden) or 1 (BMNH) plate-like scutes bearing rudimentary lateral arms (fig. 1a, b), the scutes not reaching back to the main pelvic scute (which has normal lateral arms). Snout equal to or a little shorter than eye diameter. Jaws unequal, the lower projecting slightly. Upper jaw reaching to vertical from anterior eye border or anterior pupil margin, ventral expanded portion of maxilla beginning abruptly and not tapered smoothly into slender anterior limb of bone, the entire edge of the expanded portion finely denticulated (fig. 2); a single (posterior) supra-maxilla, the lower part of the expanded portion deeper and longer than the upper part (*Harengula* shape), its depth about $\frac{1}{2}$ eye diameter. Lower jaw rising fairly steeply in the first third of its length; 6–7 small conical teeth on either side of symphysis. A single row of small conical teeth on pre-maxillae, separated by a median diastema. Fine teeth on tongue, scattered on antero-median process of palatine and along outer edge of that bone.

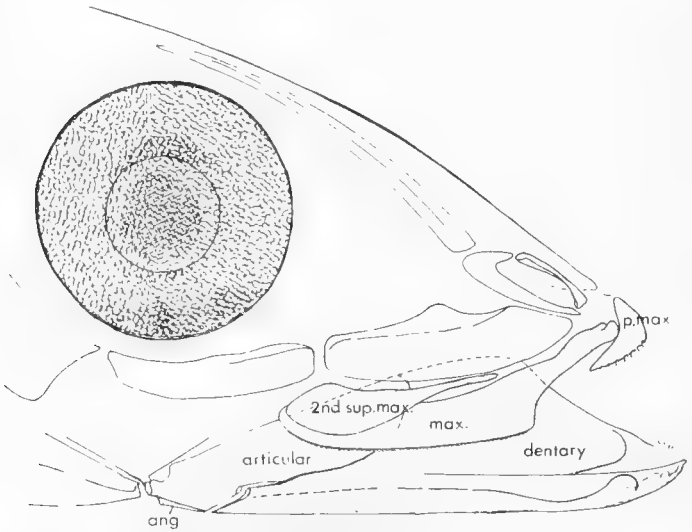


Fig. 2. *Dayella malabarica*, upper and lower jaws, alizarin stained specimen, 47·3 mm S.L., BMNH.1889.2.1.2048.

Gillrakers fine, slender, 2½ times in eye diameter and a little longer than corresponding gill filaments; about 7 short, stumpy gillrakers on posterior face of 3rd epibranchial. Pseudobranch present, exposed, about ½ eye diameter, with about a dozen filaments. Cleithral lobe present at lower angle of gill opening, fairly well developed. Operculum about 1½ times as deep as broad, its posterior margin with a deep indentation, its lower margin rising at an angle of about 15° to the horizontal; suboperculum rectangular except for rounding of postero-ventral angle. Cutaneous sensory canals branching over entire opercular series and cheek. Frontoparietal rea smooth, posterior frontal fontanelles retained and minute, 1·0 mm in length (0a·5 mm in BMNH specimen—fig. 3c; virtually occluded in Leiden specimen).

Dorsal fin origin nearer to snout tip than to caudal base by ¾ eye diameter and a little in advance of vertical from pelvic base. Pectoral fin tips failing to reach pelvic base by 1 (1½) eye diameters; no axillary scale. Pelvic fin base below first branched dorsal ray and about equidistant between pectoral base and anal origin; axillary scale present, about ⅓ of fin length (Leiden specimens). Anal fin origin a little nearer to caudal base than to pelvic base; last two rays normal, not separated from rest of fin.

Scales: deeper than broad, with distinct anterior 'shoulders'; unexposed portion with a single continuous striation, preceded by 3–4 short radiating striae (absent on anterior scales, joined to form a loop on some posterior scales); exposed portion of scale without striae, its posterior margin slightly eroded and produced medially.

Colour: in alcohol, uniform light brown with a faint silvery midlateral stripe not quite as broad as eye; fins hyaline.

NOTE. The new genus *Dayella* is a member of the pellonuline complex that comprises the monotypic Indo-Pacific genera *Ehirava, Gilchristella, Sauvagella* and *Spratellomorpha.* These five genera are distinguished from all other Indo-Pacific pellonulines by their lack of post-pelvic scutes; in addition, pre-pelvic scutes are either absent or extremely poorly developed. The separation of the five species at generic level is arguable but the features that distinguish them are non-meristic and appear to be of some significance in other groups of clupeids. *Dayella* can be identified from the following key.

INDO-PACIFIC PELLONULINAE THAT LACK POST-PELVIC SCUTES

I. Anal fin entire, last two rays not separate

A. Gillrakers present on posterior face of 3rd epibranchial

1. Posterior frontal fontanelles minute (⅕ eye diameter) or completely occluded in adults (fig. 3c); pre-pelvic scutes 1–4, rudimentary, lateral arms barely developed (fig. 1a, b); pelvic base well behind dorsal origin; gillrakers 24–27

Dayella malabarica (Day)

2. Posterior frontal fontanelles larger (⅓–½ eye diameter), retained in adults (fig. 3a, b); pelvic base before dorsal origin

a. No pre-pelvic scutes; gillrakers 19 (at 40 mm S.L.)

Sauvagella madagascariensis (Sauvage)

b. Up to 9 pre-pelvic scutes, with thin lateral arms

i. Anterior arm of supra-occipital broadening anteriorly (fig. 3b); gillrakers 39–45

Gilchristella aestuarius (Gilchrist)

ii. Anterior arm of supra-occipital very slender anteriorly (fig. 3a); gillrakers 40–60

Gilchristella sp. (see below)

B. Gillrakers absent on posterior face of 3rd epibranchial; posterior frontal fontanelles large, anterior arm of supra-occipital broadening anteriorly (fig. 3d); pre-pelvic scutes present, poorly developed but with distinct lateral arms (fig. 1d); pelvic base below or before dorsal origin; gillrakers 26–30 . . . . . ***Ehirava fluviatilis*** Deraniyagala

II. Anal fin split, the last two rays separate from rest of fin; gillrakers present on posterior face of 3rd epibranchial; posterior frontal fontanelles large, probably retained in adults, similar to those of *Ehirava*; gillrakers 26–31

Spratellomorpha bianalis (Bertin)

The four previously described Indo-Pacific genera were formerly placed in the round herrings or Dussumieriidae (Whitehead, 1963). The subsequent discovery of partially scuted (*Laeviscutella*, *Sierrathrissa*) or non-scuted (*Congothrissa*) forms amongst the otherwise fully scuted West African Pellonulinae suggested that both Indo-Pacific and African genera were members of a clupeid group that showed progressive stages in scute loss. This appeared to be correlated with trends towards reduction in supra-maxillae and numbers of branchiostegal rays, together with a retention of the posterior frontal fontanelles by adults (Poll, Whitehead & Hopson, 1965). The non-scuted genera *Spratelloides* (Indo-Pacific) and *Jenkinsia* (Western Atlantic) may eventually join this group, although their very characteristic W-shaped pelvic scute seems to link them with the 'true' round herrings *Dussumieria* and *Etrumeus*—whose high and presumably primitive branchiostegal count implies yet another route to scute loss (or perhaps the primitive absence of scutes, at least in this branch of the clupeids). For the present, the five poorly or non-scuted genera shown in the key above are placed in the tribe Ehiravini of the subfamily Pellonulinae.

In *Dayella*, the scutes are more rudimentary than in any other clupeid genus. They are thin, difficult to find in unstained material and those with small lateral arms could easily be mistaken for scales. Their resemblance to scales is increased by the relatively large size of the expanded portion of the scute when compared with those of other genera (fig. 1a–d). The variation in shape of these scutes implies that these are structures on the way to being lost and not an early stage in the evolution of scutes.

Dayella appears to be most closely allied to *Gilchristella*, *Sauvagella* and *Ehirava*, differing from them chiefly in its occluded posterior frontal fontanelles and its less advanced pelvic base. The absence of gillrakers on the posterior face of the 3rd epibranchial seems to hold some significance elsewhere in the Clupeidae, but this

may not mean that *Ehirava* is necessarily remote from the other genera of the group. The status of *Sauvagella madagascariensis* is uncertain. Re-examination of a syntype of this species (40 mm S.L., MNHN.3794) has confirmed that even the rudimentary scutes of *Dayella* are not present. This fish has only 19 gillrakers and the posterior frontal fontanelles are large, suggesting that it is a juvenile; gillrakers may increase with size. In a redescription of the species (Whitehead, 1963), eleven South African specimens were included, from the Buffalo river, Cape Province (BMNH.1878.1.22.25 and 33–43) and the stated gillraker count of 40–56 referred to these specimens only. Careful removal of the belly scales now shows that these fishes have up to 7 thin and barely apparent scutes with fairly long lateral arms. Thus, they are clearly distinct from *Sauvagella* (as far as can be judged from the very small types) and for the moment they appear to be an undescribed species of *Gilchristella*. From *G. aestuarius* they differ, however, in having a very slender

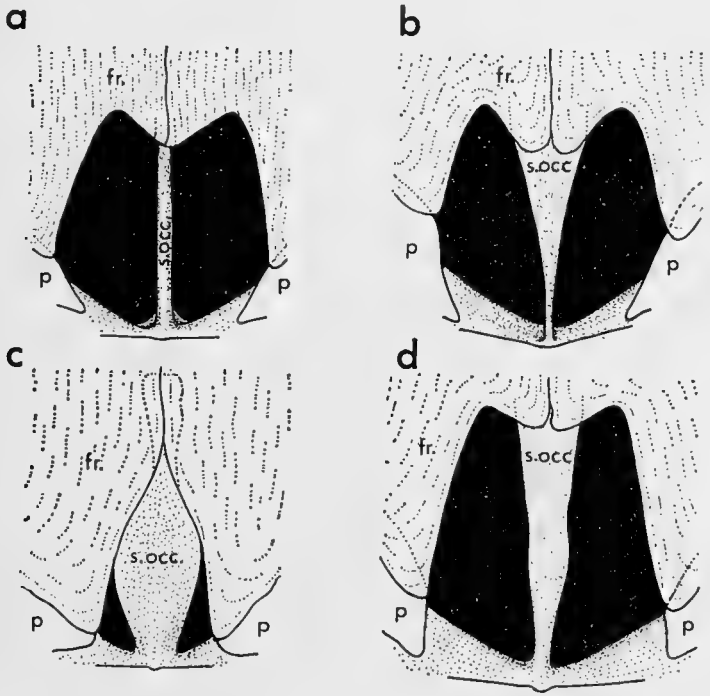


FIG. 3. Posterior frontal fontanelles in four Indo-Pacific pellonulines, dorsal view showing frontals (fr.), parietals (p.) and anterior arm of supra-occipital (s. occ.), the fontanelles black. a. *Gilchristella* sp., 52·6 mm S.L., anomalous Buffalo River specimen, BMNH.1878.1.22.25. b. *Gilchristella aestuarius*, 54·5 mm S.L., BMNH.1919.9.12.3. c. *Dayella malabarica*, 47·3 mm S.L., BMNH.1889.2.1.2048. d. *Ehirava fluviatilis*, 50·0 mm S.L., BMNH.1889.2.1.2052.

anterior arm of the supra-occipital (fig. 3a) and a higher gillraker count (40–60 cf. 39–45). In general, the members of the *Ehirava* complex are rather poorly known and would repay further study when more specimens are available.

(Subfamily ***ALOSINAE***)

3. ***Clupea variegata*** Day, 1869

= ***Gudusia variegata*** (Day, 1869)

(Plate 1c)

Clupea variegata Day, 1869, *Proc. zool. Soc. Lond.*: 623 (Irrawaddy and its branches; many specimens, to 7 inches); *Idem*, 1878, *Fishes of India*: 639, pl. 161 (4) (repeat; figure of fish 152 mm S.L., presumably life-size); *Idem*, 1889, *Fauna British India, Fishes*, **1** : 375 (repeat).

Gudusia variegata: Regan, 1917, *Ann. Mag. nat. Hist.*, (8) **19** : 308 (on single Day specimen in British Museum); Motwani, Jayaram & Sehgal, 1962, *Trop. Ecol.*, **3** (1–2) : 17–43 (Brahmaputra at Jogighopa, Goalpara District); Whitehead, 1965, *Bull. Br. Mus. nat. Hist.* (Zool.), **12** (4) : 150, fig. 11 (Day specimen redescribed; Day's figure reproduced); *Idem*, (in press), *Symp. Indian Ocean Adj. Seas. Mar. biol. Ass. India* (key, note on synonymy).

? *Clupea suhia* Chaudhuri, 1912, *Rec. Indian Mus.*, **7** : 436, pl. 38 (1) (river Gandak in Saran, Bihar).

? *Gudusia godanahiai* Srivastava, 1968, *Fishes Eastern Uttar Pradesh*: 6, fig. 4a, b (Gorakhpur, Uttar Pradesh).

Material.

a. ZSI.2245, a fish 150·0 mm S.L., *ex* Irrawaddy river (stated to be basis for Day's figure—LECTOTYPE)
b. ZSI (Duplicate Cat.) 43, a fish 158 mm S.L., *ex* Bassein river (labelled *Clupea burmanica*)
c. ZSI. (Duplicate Cat.) 168, a fish 78 mm S.L., *ex* Mandalay, coll. Major E. B. Sladen (labelled *Clupea burmanica*)
d. AMS.B7676, a fish 158·5 mm S.L. (191 mm tot. l.), *ex* Bassein (claimed as type by Whitley, 1958.
e. NHMV (no specimens)
f. RMNH.2586, a fish 106·4 mm S.L., *ex* Bassein.
g. ZMB (no specimens)
h. BMNH.1870.6.14.38, a fish 155 mm S.L., *ex* Bassein.

For reasons given under the previous two species, the figured specimen in Calcutta is chosen as lectotype. The two specimens labelled '*burmanica*' are *G. variegata* but are probably not syntypes since their meristic counts exceed the values given in the original description (but are consistent with the ranges given in the *Fishes of India*). Day did not publish the name *burmanica* but may have initially intended to use it for this species. The British Museum specimen, although presented in 1870 and thus the first of this species to be given away by Day, has too low an anal and pectoral count (iii 22 and i 13; cf. iii 26 and i 15) to have figured in the original

description, which in any case seems to have been based on a single specimen (although many were taken). For this reason, the Sydney and Leiden specimens cannot be regarded as paralectotypes.

DESCRIPTION. Based on the LECTOTYPE, a fish 150·0 mm S.L., *ex* Irrawaddy river, ZSI.2245 (basis for pl. 161 (4) of *Fishes of India*).

Br. St. 6, D iii 12, P i 15, V i 7, A iii 26, g.r. 210 (approx.), scutes 19 + 11, scales in lateral series 90, transverse 35.

In percentages of standard length: body depth 44·3, head length 29·3; snout length 5·5, eye diameter 6·7, length of upper jaw 11·7, length of lower jaw 13·0, operculum height 14·3, its breadth 8·3; pectoral fin length 20·0, pelvic fin length 10·0, length of anal fin base 23·0; pre-dorsal distance 52·0, pre-pelvic distance 54·7, pre-anal distance 74·0.

Body strongly compressed, its width $3\frac{3}{5}$ times in its depth, the latter $1\frac{1}{2}$ times head length; belly keeled, tips of scutes projecting slightly from sheath of scales on either side. Snout shorter than eye diameter; pre-orbital distance (including eye) $\frac{3}{4}$ of post-orbital distance. Lower jaw included when mouth closed; pre-maxillae rising steeply to form very distinct notch in upper jaw. Maxilla reaching to just beyond vertical from eye centre, expanded portion without longitudinal ridges or striae and smooth along lower edge; two supra-maxillae, the 1st (anterior) about 6 times as long as deep and almost equal in length to eye diameter, the 2nd (posterior) with slender anterior shaft and lower part of expanded portion larger than upper. Lower jaw rising rather gently in the first third of its length, its depth about 3 times in its length; no teeth present. No teeth in upper jaw nor within mouth.

Gillrakers fine, straight or slightly curved, slightly longer than corresponding filaments; filaments of anterior hemibranch of 1st arch $\frac{1}{2}$–$\frac{3}{4}$ length of those of posterior hemibranch; many fine gillrakers present on posterior face of 3rd epibranchial. Medio-pharyngobranchial present, about $\frac{3}{4}$ eye diameter, bearing many short gillrakers. Pseudobranch present, attenuated, about $1\frac{4}{5}$ times eye diameter, with distinct ventral ridge and a groove below it. Cleithral lobe barely developed, hardly breaking outline of gill opening. Operculum not quite twice as deep as broad, its lower edge rising steeply; sub-operculum crescentic; lower third of anterior operculum margin not overlapped by pre-operculum, leaving a small triangular area covered only by skin. Cutaneous sensory canals branching through the adipose tissue covering the suborbitals, operculum, sub-operculum and scales behind head. Adipose eye-lid with vertical slit exposing $\frac{3}{4}$ of pupil. Dorsal surface of head covered by fairly thick skin but a pair of cuneiform fronto-parietal areas with about six longitudinal striae left exposed.

Dorsal fin origin slightly nearer to snout tip than to base of caudal; a very low scaly sheath along base. Pectoral fin tips failing to reach pelvic base by about $\frac{1}{2}$ eye diameter; axillary scale present, half length of fin. Pelvic fin base below vertical from dorsal origin and a little nearer to pectoral base than to anal origin; axillary scale present, half length of fin. Anal origin equidistant between pelvic and caudal bases; anal base longer than pectoral fins and greater than the distance

snout tip to posterior border of pre-operculum. Caudal fin (broken) slightly longer than head length, lower lobe longer than upper.

Scales: almost circular, but becoming more elongate on posterior part of body; a single vertical striation continuous across scale, preceded by 0 (anterior scales) to 3 (posterior scales) short and irregular striae interrupted at centre of scale; exposed border irregular, becoming pectinate in posterior scales. Minute scales covering caudal except for hind border.

Colour: in alcohol, back brown, flanks golden; a series of brown spots along upper flank, some expanded vertically, those behind dorsal extending right across back; a dark humeral spot.

NOTE. The genus *Gudusia* (often misspelt *Gadusia* in the literature) at present includes two species, *G. chapra* (Ham. Buch.) and *G. variegata*. The latter has a deeper body (depth greater than 40% of S.L.), a shorter head (head length less than 28% of S.L.), and more anal finrays (iii 22–26; cf. iii 19–22). In addition, *G. variegata* has a very prominent series of black spots along the flank, whereas *G. chapra* is usually described as having a dark shoulder spot, sometimes absent, and faint or no spots along the flank (Whitehead, 1965; Srivastava, 1968). Rather few specimens of *G. variegata* have been described, however, and some of these were misidentifications. Thus, specimens identified as *G. variegata* from Akyab by Lloyd (1907) include at least one fish (ZSI.1491/1) that is *Hilsa kelee*, while juveniles reported as *G. variegata* from the Mandalay fish market by Jenkins (1910) include specimens (ZSI.1770/1) of a species of *Hilsa* (*Tenualosa*).

Gudusia variegata is usually considered a Burmese species (Regan, 1917b; Fowler, 1941 : 635), but both Chandhuri's *Clupea suhia* and Srivastava's *Gudusia godanahiai* (Ganges drainage) had very prominent black spots along the flanks which were, indeed, the main reason for distinguishing these nominal species from the sympatric and unspotted *G. chapra* (not a sexual feature according to Srivastava, 1968). *Gudusia variegata* has also been reported from the Brahmaputra, by Motwani *et alii* (1962), presumably because of the strong pattern of spots since *G. chapra* was also recorded from the same area (no descriptions given, however). If these Indian records truly relate to *G. variegata*, then some modification must be made to the key since Srivastava's *G. godanahiai* were rather slender (depth 33·3–38·7% of S.L.) and thus within the range of *G. chapra* (31·0–40·0% in 30 specimens—Whitehead, 1965: fig. 13); the head length (27·4–31·7% of S.L.) of Srivastava's specimens, however, agreed with current definitions of *G. variegata*, but the low anal count of ii–iii 20 was that of *G. chapra*. Srivastava distinguished his new species by the presence of 14 pectoral rays (13 in his *G. chapra*), but Regan (1917b) recorded 13–14 pectoral rays in the British Museum material of *G. chapra* and there is probably overlap between the two species. For the present, the status of *G. variegata* and its possible synonyms must remain uncertain until more material has been examined.

(Subfamily ***DOROSOMATINAE***)

4. *Chatoessus modestus* Day, 1869

= *Gonialosa modesta* (Day, 1869)

Chatoessus modestus Day, 1869, *Proc. zool. Soc. Lond.*: 622 (Bassein river as high as Een-gay-gyee Lake; many specimens, up to 5½ inches); *Idem*, 1878, *Fishes of India*: 633, pl. 160 (1) (also Selwein at Moulmein; figure of fish 100·1 mm S.L., ? life size); *Idem*, 1889, *Fauna British India, Fishes*, **1** : 386 (repeat).

Gonialosa modesta: Regan, 1917, *Ann. Mag. nat. Hist.*, (8) **19** : 315 (on Day material in British Museum); Menon & Yazdani, 1963, *Rec. zool. Surv. India*, **61** : 98.

Material.

a. ZSI.2695, a fish 98·0 mm S.L., *ex* Bassein river (stated to be basis for Day's figure—LECTOTYPE)
b. ZSI.F8022/1 and 8023/1, two fishes 58·0–101·0 mm S.L., *ex* Bassein river (= *G. manminna*)
c. AMS.B7637, a fish 105·0 mm S.L. (127·5 mm tot. l.), *ex* Burma (claimed as type by Whitley)
d. NHMV (no specimens)
e. RMNH.2585, a fish 116·0 mm S.L., *ex* Moulmein (claimed as type in register)
f. ZMB (no specimens)
g. BMNH.1889.2.1.1879, a fish 82·6 mm S.L., *ex* Burma

Menon & Yazdani (1963) erroneously listed the first of the three Zoological Survey fishes as holotype, and the other two as paratypes, but Day did not indicate a holotype nor did he give an exact length measurement. The first Calcutta specimen, used for Day's figure, is here designated lectotype; the other two are *G. manminna* and thus do not agree with the original description, which in any case shows no ranges for meristic and morphometric values, suggesting that only a single fish was measured (although many were caught). For this reason, the Sydney, Leiden and London specimens are not regarded as paralectotypes.

Description. Based on the LECTOTYPE, a fish 98·0 mm S.L., *ex* Bassein river, ZSI.2695 (basis for pl. 160 (1) of *Fishes of India*).

Br. St. 6, D iii 13, P i 15, V i 7, A iii 25, g.r. 150 (approx.), scutes 17 + 12, scales in lateral series 47, transverse 17.

In percentages of standard length: body depth 48·5, head length 27·6; snout length 6·4, eye diameter 7·9, post-orbital distance 13·3, length of upper jaw 7·1, length of lower jaw 9·7; pectoral fin length 23·0, pelvic fin length 10·2, length of anal base 26·8; pre-dorsal distance 52·0, pre-pelvic distance 50·0, pre-anal distance 72·4.

Body compressed, its width $4\frac{7}{10}$ times in its depth, the latter almost twice head length; belly keeled, tips of scutes projecting below scaly sheath; profile of back concave beyond nape, rising abruptly to dorsal origin, belly profile evenly convex. Snout shorter than eye diameter. Mouth sub-terminal, transverse, with snout projecting strongly; pre-maxillae meeting at an angle to form a distinct notch in

upper jaw. Maxilla slender, slightly expanded and curved downwards distally, reaching to vertical from anterior border of eye; a single narrow supra-maxilla, its length 2·5 mm and depth 0·5 mm. Lower jaw with dentaries meeting at an obtuse angle, the edge of each dentary flared or reflected outwards in front of tips of maxillae. No teeth in jaws.

Gillrakers very fine, close-set, shorter than corresponding gill filaments and slightly more than $\frac{1}{3}$ eye diameter; gill filaments of anterior hemibranch equal to those of posterior hemibranch. Numerous fine and close-set gillrakers on posterior face of 3rd epibranchial. Pseudobranch present, exposed, its length almost one eye diameter; about 20 filaments present. Cleithral lobe present, breaking outline of gill opening but not strongly developed. Operculum $1\frac{1}{2}$ times as deep as broad, its lower border rising steeply (about 40°); suboperculum long and narrow, its posterior border rounded. Cutaneous sensory canals branching over cheek, opercular series and nape. Adipose eye-lid with vertical slit exposing $\frac{1}{3}$ of eye. Dorsal surface of head with a pair of cuneiform fronto-parietal areas bearing 6 longitudinal striae, the two areas linked posteriorly by a transverse bony ridge.

Dorsal fin origin slightly nearer to snout than to base of caudal fin; final finray not elongated. Pectoral fin tips reaching to beyond pelvic base; axillary scale present, $\frac{1}{4}$ length of fin. Pelvic fin base in front of dorsal origin and nearer to pectoral base than to anal origin; axillary scale present, $\frac{1}{3}$ length of fin. Anal origin nearer to pelvic than to caudal base. Lower lobe of caudal larger than upper.

Scales: unexposed portion with one major vertical striation and 3 (anterior scales) to 4–5 (posterior) minor vertical striae interrupted at scale centre. Exposed portion without striae, posterior margin of scale not eroded, perforated or fimbriated.

Colour: in alcohol, upper parts of body light brown, lower parts silvery; a dark humeral spot present. Fins hyaline.

NOTE. The two species of *Gonialosa*, *G. modesta* and *G. manminna* (Ham. Buch.), have been separated on body depth (40–50% of S.L. in *modesta*; 30–39% in *manminna*) and number of scales along the flank (45–47 and 55–65 respectively—Whitehead, 1962; in press). *Gudusia manminna* (from the Ganges and Brahmaputra and their tributaries) is fairly well represented in collections and the literature, but *G. modesta* (recorded only from Burma) is not. Larger collections may show *modesta* to be merely a subspecies of *G. manminna*.

(Subfamily ***PRISTIGASTERINAE***)

5. ***Pellona sladeni*** Day, 1869

= ***Ilisha sladeni*** (Day, 1869)

Pellona sladeni Day, 1869, *Proc. zool. Soc. Lond.*: 623 (Irrawaddy at Mandalay; specimens up to 7 inches); *Idem*, 1878, *Fishes of India*: 645, pl. 164 (1) (repeat; 'A single example obtained, 7 inches in length'; figure shows fish of 146 mm S.L.); *Idem*, 1889, *Fauna British India, Fishes*, **1** : 383 (repeat).

Ilisha sladeni: Norman, 1923, *Ann. Mag. nat. Hist.*, (9), **11** : 6 (Day specimen and two others described).

MATERIAL.

a. ZSI.2672, a fish 210 mm S.L. (ca. 10 inches tot. l.), *ex* Irrawaddy (stated to be basis for Day's figure—LECTOTYPE)
b. ZSI (Duplicate Cat.) 298, a fish 189 mm S.L. (ca. 8½ inches tot. l.), *ex* Mandalay (? PARALECTOTYPE)
c. AMS (no specimens)
d. NHMV (no specimens)
e. RMNH (no specimens)
f. ZMB (no specimens)
g. BMNH.1870.6.14.36, a fish 209 mm S.L. (almost 10 inches tot. l.), *ex* Mandalay.

As in previous cases, Day clearly collected more than one specimen, but he gave no ranges for meristic or morphometric values in his original description. In the *Fishes of India*, however, he stated 'single example obtained'; he may perhaps have been referring to the fish that he himself had drawn for the *Fishes of India*, since it was now eight years since he had given his other specimen to the British Museum. All three extant specimens are larger than either the figure or the maximum length stated (7 inches). They also differ in having more pre-pelvic scutes (23 or 24; cf. 20) and more pectoral rays (14 or 15; cf. 11). Day altered his scute count to 23 in the *Fishes of India* (but not the pectoral count) and it must be presumed that the earlier counts were errors. The larger Calcutta fish, the figured specimen, is chosen as lectotype, on the assumption either that Day lost the original (smaller) specimen or that the maximum length of 7 inches was also an error.

DESCRIPTION. Based on the LECTOTYPE, a fish 210 mm S.L., *ex* Irrawaddy river, ZSI.2672 (basis for pl. 164 (1) of *Fishes of India*) (measurements of ZSI paralectotype given in parenthesis).

Br. St. 6, D iii 10, P i 13, V i 6, A iii 41, g.r. 10 + 1 + 21, scutes 23 + 10, scales in lateral series 48, transverse 10.

In percentages of standard length: body depth 21·9 (25·4), head length, 24·5 (27·5); snout length 5·5 (5·8), eye diameter 6·0 (6·6), length of upper jaw 11·0 (11·9), length of lower jaw 11·4 (13·0); pectoral fin length 19·8 (21·7), pelvic fin length 4·8 (6·6), length of anal fin base 30·0 (29·4); pre-dorsal distance 59·1 (59·3), pre-pelvic distance 39·1 (44·0), pre-anal distance 65·2 (67·2).

Body strongly compressed, its width 4 times in its depth, belly strongly keeled, the tips of the scutes projecting below scaly sheath, especially behind pelvic fin base; anterior four scutes on isthmus. Dorsal profile slightly concave before nape, ventral profile evenly convex, the two almost parallel between pectoral base and dorsal origin. Snout a little shorter than eye diameter. Lower jaw strongly projecting, about ½ eye diameter beyond snout when mouth closed. Maxilla reaching to vertical from anterior pupil border, fine denticulations along its lower edge; no hypo-maxilla; two supra-maxillae, the 1st (anterior) 5 times longer than deep and about 1½ eye diameter, the 2nd (posterior) with lower lobe of expanded portion much larger than upper. A single series of fine teeth on pre-maxillae, with median diastema, small conical teeth present on either side of dentary symphysis. No teeth on vomer but fine teeth on tongue, palatines and ecto- and endo-pterygoids.

Gillrakers fairly slender, the longest $\frac{1}{2}$ eye diameter and $1\frac{1}{2}$ times length of corresponding gill filaments; no gillrakers on posterior face of 3rd epibranchial. Pseudobranch present, exposed, its length $\frac{1}{2}$ eye diameter; ventral margin not ridged. No cleithral lobe. Operculum elongated posteriorly, its ventral margin equal to its height and rising at an angle of about 20°; sub-operculum eliptical, long and narrow, its height $3\frac{7}{10}$ times in its width; lower border of sub-operculum and hind border of inter-operculum almost parallel to upper profile of head, to leave a broad triangular area below (bounded posteriorly by base of pectoral fin). Dorsal surface of head with two prominent longitudinal striae, diverging slightly posteriorly, flanked by two small lateral striae over eyes.

Dorsal fin origin set far back on body, equidistant between caudal base and posterior margin of operculum. Pectoral fin tips reaching almost to tips of pelvics; axillary scale present, $\frac{1}{3}$ length of fin. Pelvic base nearer to pectoral base than to anal origin by 2 eye diameters; axillary scale present, about $\frac{1}{3}$ length of fin. Anal fin origin below vertical from anterior third of dorsal base; base of fin covered by low scaly sheath.

Scales: unexposed portion with a single complete W-shaped vertical striation, preceded by 3 (anterior scales) to 6 (posterior) shorter striae interrupted at centre of scale; exposed portion with about 16 very short radiating striae at edge of scale, not discernible in posterior scales.

Colour: in alcohol, upper $\frac{1}{3}$ of body brown, rest of flanks silvery; fins hyaline, hind margin of caudal dusky. Inner face of operculum slightly dusky.

NOTE. *Ilisha sladeni* closely resembles *I. pristigastroides* (Bleeker), with which it has been synonymized (Whitehead, 1970), but comparison of Day's material with Bleeker's type in the British Museum (1867.11.28.12—redescribed in Whitehead *et alii*, 1966) suggests that I. *sladeni* is distinct. In both species the anal origin is well before the vertical from the midpoint of the dorsal base, a feature used in keys to separate these species from all other *Ilisha* (Whitehead *et alii*, *loc. cit.*; Whitehead, 1970). The type of *I. pristigastroides* is a smaller fish (151 mm S.L.; cf. 189–210 mm in the Day material), but this does not account for its deeper body (30·8% of S.L.; cf. 21·9, 25·4 and 22·4% in the Day material) since a larger Bleeker specimen (302 mm S.L., BMNH.1867.11.28.9) is still deeper-bodied (30·9% of S.L.) than a similar large specimen of *I. sladeni* (25·9% in a fish of 308 mm S.L., *ex* Sittang river, Burma, BMNH.1891.11.30.402). The Bleeker type also has a relatively longer anal base (41·1% of S.L.; cf. 30·0, 29·4 and 30·8%), the anal origin being set further back on the body (equidistant between caudal base and eye centre; cf. nearer to caudal base than to pectoral base), and the dorsal origin is also correspondingly less far back on the body. In spite of the more compact body in *I. pristigastroides*, there are more pre-pelvic scutes (26) than in the elongate *I. sladeni* (23–24). All these features also serve to separate the two larger specimens mentioned above.

A striking feature of *I. sladeni*, to some extent shared by the type of *I. pristigastroides*, is the very elongate appearance of the head, shown well in Day's drawing (see Pl. 2). This is partly due to the length of the head but more particularly to

the more squat operculum (its height just over $2\frac{1}{2}$ times in head length; cf. $2–2\frac{1}{4}$ times in other species). Also, the depth of the head, taken at right angles to the profile at the occiput, is much less ($1\frac{2}{3}$ times in head length) than in other species ($1\frac{1}{4}–1\frac{1}{2}$ times).

A further difference between *I. sladeni* and *I. pristigastroides* is in the form of the swimbladder. In *I. sladeni* the swimbladder terminates at the posterior end of the body cavity (BMNH specimens of 209 and 308 mm S.L.), whereas in *I. pristigastroides* there is a postcoelomic, tapering prolongation down the right side of the body lateral to both the haemal spines and the anal pterygiophores and reaching as far as the level of the 15th branched anal ray. The condition in *I. sladeni* appears to be unique amongst Indo-Pacific members of *Ilisha* but it is found in the South American *I. furthii* (and probably also in the related *I. amazonica*—no BMNH specimens). The asymmetrical postcoelomic prolongation in *I. pristigastroides* is similar to that found in the Indo-Pacific *I. elongata* and *I. megaloptera*; in *I. africana* (West Africa) and *I. indica* (Indian Ocean) the prolongation of the swimbladder is bifid.

Family *ENGRAULIDAE*

6. *Engraulis auratus* Day, 1865

= *Thryssa dussumieri* (Valenciennes, 1848)

(Plate 2)

Engraulis dussumieri Valenciennes, 1848, *Hist. Nat. Poiss.*, **21** : 69 (no locality; putative neotype described by Whitehead, 1967 : 142); Day, 1878, *Fishes of India*: 627, pl. 158 (4) (*E. auratus* in synonymy); *Idem*, 1889, *Fauna British India, Fishes*, **1** : 391.

Thryssa dussumieri: Whitehead (in press), *Symp. Indian Ocean Adj. Seas. Mar. biol. Ass. India* (key, synopsis, fig.).

Engraulis auratus Day, 1865, *Proc. zool. Soc. Lond.*: 312 (Cochin on Malabar coast; on specimen $4\frac{6}{10}$ inches = 117 mm); *Idem*, 1865, *Fishes of Malabar*: 238, pl. 19 (2) (repeat; fig. (? life-size) $4\frac{1}{2}$ inches = 114·7 mm tot. l.).

MATERIAL.

a. ZSI (no specimens)
b. AMS (no specimens and none in *Great Fisheries Exhibition Catalogue* by Day, 1883)
c. NHMV (no specimens)
d. RMNH (no specimens)
e. ZMB.10412, a fish 89·7 mm S.L. (109·2 mm tot. l.), *ex* Bombay
f. BMNH.1867.5.30.13, a fish 83·1 mm S.L. (99·4 mm tot. l., caudal lobes damaged, estimated 103·3 mm), *ex* Madras, coll. Day
g. BMNH.1889.2.1.1779, a fish 90·6 mm S.L. (112·7 mm tot. l., caudal complete), *ex* Malabar, coll. Day (outside label altered from *E. auratus* to *mystax* Gthr.) (label inside jar, *Engraulis auratus* Malabar), LECTOTYPE

h. BMNH.1889.2.1.1780, a fish 55·2 mm S.L. (68·9 mm tot. l., caudal complete), *ex* Canara, coll. Day (label in jar, *Engraulis auratus* Canara)

In the *Fishes of Malabar* (p. vi) it is stated that a specimen of *E. auratus* had been deposited in the East India Museum (but apparently not in the British Museum). Manuscript catalogues and lists of zoological material presented to the museum of the East India Company are now in the British Museum (Natural History). One list of fishes is headed 'The following families are from Day's Malabar Fishes' and it includes *Engraulis auratus* from Malabar (preceded by the number 5, which seems to be an indication of the number of specimens). When the India Museum was dispersed in 1879, at least two of Day's presentations (birds and fish skins) were sent back to Day. Since no fishes were given to the British Museum at that time, Day probably also received back his spirit specimens, including *Engraulis auratus*. It is possible, therefore, that the specimen (or one of them) is that now in London and presented in 1889 (specimen g above).

There is a discrepancy of 2·3 mm between the length of the single specimen described in the original description and the length of the figure, which suggests that the figure was not exactly life-size. Since all four extant specimens are too small and there can be no certainty which, if any, contributed to the original description, we have chosen the British Museum Malabar specimen (g above) as lectotype.

Description. Based on the LECTOTYPE, a fish 90·6 mm S.L. (112·7 mm tot. l.) in good condition, *ex* Malabar, BMNH.1889.2.1.1779.

Br. St. 11, D I iii 10, P i 11, V i 6, A iii 32, g.r. 15 + 18, scutes 15 + 7.

In percentages of standard length: body depth 27·8, head length 26·9; snout length 3·6, eye diameter 6·4, length of upper jaw 41·1, length of lower jaw 19·3; pectoral fin length 18·1, pelvic fin length 11·1, length of anal base 33·0; pre-dorsal distance 49·0, pre-pelvic distance 42·2, pre-anal distance 59·3.

Body compressed, its width 3 times in its depth, the latter only slightly greater than head length; belly not strongly keeled, all but tips of scutes concealed by scaly sheath; head profile rising steeply from snout to nape and then more gradually to dorsal origin, belly profile evenly convex. Snout short, about $\frac{2}{3}$ eye diameter. Upper jaw very long, the right maxilla pointed posteriorly, reaching to pelvic base and about $\frac{4}{5}$ along pectoral fin (tip of left maxilla broken off); expanded portion of maxilla tapering rapidly behind 2nd supra-maxilla but with a membrane along upper edge; 2nd (posterior) supra-maxilla with upper part of expanded portion larger than lower; no 1st (anterior) supra-maxilla. Dentary symphysis below mid-point between eye and tip of snout; articulation of lower jaw $\frac{1}{2}$ eye diameter behind 2nd supra-maxilla. A single series of fine conical teeth on dentaries, pre-maxillae and along lower edges of maxillae except near tip; two (right) and three (left) conical teeth on vomer; fine granular teeth on tongue, palatines and on endo- and ecto-pterygoids.

Gillrakers fine, slender, the longest $1\frac{1}{4}$ times length of corresponding gill filaments and almost equal to eye diameter; 8 short, triangular rakers on posterior face of 3rd epibranchial: gillraker serrae on both 1st and 2nd arches in distinct clumps,

with the longest serae in the middle of each clump. Pseudobranch present, concealed by skin but with small posterior opening. Isthmus silvery, not bearing anterior members of scute series, tapering evenly to just behind posterior margin of branchiostegal membrane. Operculum $3\frac{1}{2}$ times as deep as broad, its posterior margin evenly rounded and not completely covering gill opening. Dorsal surface of head covered by thick layer of skin with numerous pores; posterior frontal fontanelles present, long and narrow, 2·1 mm by 0·5 mm (right).

Dorsal fin origin nearer to snout than to caudal base by 1 eye diameter; fin preceded by a small scute-like plate bearing a retrorse spine. Pectoral fin reaching just over $\frac{2}{3}$ along pelvic fin; axillary scale present, just over half length of fin. Pelvic fin base 1 eye diameter before vertical from dorsal origin and much nearer to pectoral base than to anal origin; axillary scale present, $\frac{4}{5}$ length of fin; a second triangular scale present, below fin, $\frac{1}{2}$ length of fin. Anal origin $\frac{3}{4}$ eye diameter behind vertical from last dorsal ray. Caudal peduncle a little deeper than long.

Scales: distinct anterior and posterior 'shoulders' to scale; unexposed portion with 10–12 irregular vertical striae, not interrupted at centre of scale, exposed portion with one semicircular striation but more frequently reticulated, especially in posterior scales, the reticulations finally covering the whole scale. Many elongate scales at base of caudal but no true alar scales.

Colour: general body colour silvery/gold, but brown where scales lost; dark brown venulose humeral area with peppering of dark pigment across back (as in Day's figure—see Pl. 2c). Fins hyaline except for narrow dark posterior border to caudal.

Note. The long maxilla, absence of the 1st supra-maxilla and distinct clumping of the gillraker serrae are characteristic of *Thryssa dussumieri* (descriptions in Whitehead, 1967 : 142, fig. 14c and 1968 : 23, fig. 2a), and Day (1878) later placed his *auratus* in the synonymy of that species.

TABLE 1

The clupeoid fishes in Day's *Fishes of India* and Day material in Calcutta, Sydney, London, Vienna, Berlin and Leiden

*present in collection (registration number given for possible types)

Species in *Fishes of India*	page	fig.	Identification	Zool. Survey, Calcutta	Austr. Mus., Sydney	Brit. Mus., London	Naturhist. Mus., Vienna	Zool. Mus., Berlin	Rijksmus., Leiden
CHIROCENTRIDAE									
Chirocentrus dorab	652	166 (3)	*Chirocentrus dorab* (Forssk., 1775)	*	*	*		*	*
CLUPEIDAE									
(Dussumieriinae)									
Dussumieria acuta	647	166 (4)	*Dussumieria acuta* Val., 1847	*	*	*		*	*
Dussumieria hasseltii	647	166 (5)	*Dussumieria acuta* Val., 1847	*	*				(as *elopsoides*)
(Clupeinae)									
Clupea klunzei	636	163 (1)	*Herklotsichthys punctatus* (Rüpp., 1837)	*	*	(as *moluccensis*)	*		
Clupea longiceps	637	161 (2)	*Sardinella longiceps* Val., 1847	*	*	*		*	*
Clupea melanura	641	—	*Sardinella melanura* (Cuv., 1829)						*
Clupea atricauda	636	164 (5)	*Sardinella melanura* (Cuv., 1829)	*		*	*		
Clupea brachysoma	635	163 (3)	*Sardinella brachysoma* Blkr., 1852		*		*		
Clupea fimbriata	637	161 (3)	*Sardinella fimbriata* (Val., 1847)	*	*	*	*	*	*
Clupea sindensis	638	163 (2)	*Sardinella sindensis* (Day, 1878)	ZSI.2630	AMS.B7642	BNMH.1889 2.1.1919–24		ZMB.10554 (as *venenosa*)	RMNH.2519
Clupea leiogaster	636	—	*Sardinella leiogaster* Val., 1847						
Clupea lile	638	162 (1)	*Escualosa thoracata* (Val., 1847)	*	*	(also as *argyrotaenia*)	*		

Corica soborna	642	162 (5)	*Corica soborna* Ham. Buch., 1822		*	*			*
(Pellonulinae)									
Spratelloides malabaricus	648	161 (5)	*Dayella malabarica* (Day, 1873)	ZSI.2246		BMNH.1889.2.1.2048	(see also p. 85)		RMNH.2726
			Ehirava fluviatilis Deraniyagala, 1929		AMS.B8288	BMNH.1889.2.1.2050–5		ZMB.10413	
(Alosinae)									
Clupea kanagurta	640	162 (4)	*Hilsa kelee* (Cuv., 1829)		*			*	
Clupea ilisha	640	162 (3)	*Hilsa ilisha* (Ham. Buch., 1822)	*	*	*	*	*	*
Clupea toli	641	162 (2)	*Hilsa toli* (Val., 1847)	*	*	*	*	*	
Clupea chapra	639	161 (1)	*Gudusia chapra* (Ham. Buch., 1822)	*	*	*		*	*
Clupea variegata	639	161 (4)	*Gudusia variegata* (Day, 1869)	ZSI.2245	AMS.B7676	BMNH.1870.6.14.38			RMNH.2586
(Dorosomatinae)									
Chatoessus nasus	634	160 (4)	*Nematalosa nasus* (Bloch, 1795)	*	*	*	*	*	*
Chatoessus manmina	633	160 (2)	*Gonialosa manmina* (Ham. Buch., 1822)	*	*	(as *cortius*)	*	*	*
Chatoessus modestus	633	160 (1)	*Gonialosa modesta* (Day, 1869)	ZSI.2695	AMS.B7637	BMNH.1889.2.1.1879			RMNH.2585
Chatoessus chacunda	632	160 (3)	*Anodontostoma chacunda* (Ham. Buch., 1822)	*	*	*	*		*
(Pristigasterinae)									
Pellona ditchela	644	165 (5)	*Pellona ditchela* Val., 1847	*		*	*		*
Pellona hoevenii	644	165 (6)	*Pellona ditchela* Val., 1847						
Pellona elongata	643	164 (3) / 165 (1)	*Ilisha elongata* (Benn., 1830)	*	*	*	*		
Pellona leschenaulti	646	—	*Ilisha elongata* (Benn., 1830)						
Pellona indica	644	164 (4)	*Ilisha indica* (Swain., 1839)	*	(as *ditchoa*)	(as *ditchoa*)	*		
Pellona motius	643	165 (3)	*Ilisha indica* (Swain., 1839)		*	*			*
Pellona brachysoma	645	164 (2)	*Ilisha indica* (Swain., 1839)	*		*			

Pellona megaloptera	645	165 (2)	*Ilisha megaloptera* (Swain., 1839)	*	*					
Pellona filigera	643	165 (4)	*Ilisha megaloptera* (Swain, 1839)	*	*	*	*			*
Pellona sladeni	645	164 (1)	*Ilisha sladeni* (Day, 1869)	ZSI.2672		BMNH.1870. 6.14.36				
Opisthopterus tardoor	646	163 (5)	*Opisthopterus tardoore* (Cuv., 1829)	*	*	*				*
Raconda russelliana	646	163 (4)	*Raconda russeliana* Gray, 1831		*	*	*			*
ENGRAULIDAE										
Engraulis tri	630	158 (6)	*Stolephorus tri* (Blkr., 1852)	*	*	*				*
Engraulis indicus	629	158 (3)	*Stolephorus indicus* (van Hass., 1823)	*	*	(as *russellii*)	*			*
Engraulis commersonianus	629	158 (1)	*Stolephorus commersonii* (Lac., 1803)	*	*	*	*	*		*
Engraulis boelama	626	158 (7)	*Thrissina baelama* (Forssk., 1775)	*	*	*	*			
Engraulis setirostris	626	—	*Thryssa setirostris* (Prouss., 1782)							
Engraulis mystax	625	157 (3)	*Thryssa mystax* (Schn., 1801)	*	*	*	*	*		*
Engraulis purava	628	157 (2)	*Thryssa purava* (Ham. Buch., 1822)	*	*	*	*	*		*
Engraulis dussumieri	627	158 (4)	*Thryssa dussumieri* (Val., 1848)			BMNH.1867. 5.30.13 (*auratus*)	*	ZMB.10412 (*auratus*)		
Engraulis hamiltonii	625	157 (4)	*Thryssa hamiltonii* (Gray, 1835)	*	*	*		*		*
Engraulis malabaricus	625	157 (5)	*Thryssa malabarica* (Bloch, 1795)	*	*	*				*
Engraulis kammalensis	626	157 (1)	*Thryssa kammalensis* (Blkr., 1849)	*	*		*			
Engraulis taty	628	158 (5)	*Setipinna taty* (Val., 1848)			*				*
Engraulis telara	627	158 (2)	*Setipinna phasa* (Ham. Buch., 1822)	*	*	*	*	*		*
Engraulis breviceps	628	—	*Setipinna breviceps* (Cantor, 1850)							

Coilia ramcarati	631	159 (2)	*Coilia ramcarati* (Ham. Buch., 1822)	*	*	*			
Coilia cantoris	631	—	*Coilia ramcarati* (Ham. Buch., 1822)						
Coilia quadragesimalis	631	—	*Coilia ramcarati* (Ham. Buch., 1822)						
Coilia reynaldi	630	—	*Coilia reynaldi* Val., 1848						
Coilia borneensis	632	159 (1)	*Coilia reynaldi* Val., 1848	*	*				*
Coilia dussumieri	631	158 (8)	*Coilia dussumieri* Val., 1848	*	*	*			*
55 clupeoid species listed by Day			46 valid species amongst those recognized by Day	Calcutta, 39 species	Sydney, 40 species	London, 41 species	Vienna, 23 species	Berlin, 18 species	Leiden, 32 species

Note: Dr. Gareth Nelson is describing a new species of *Nematalosa*, close to *N.nasus*. One of Day's specimens of *N.nasus* in the British Museum is this new species, *ex* Canara, BMNH. 1889.2.1. 1877.

REFERENCES

ANON. 1885. *Australian Museum* (*Report of the Trustees for* 1884). Govt. Printer, Sydney, 46 pp. App. XI (p. 29)—report by E. P. Ramsey; (pp. 42–46)—list of Day specimens.

—— 1886. *Australian Museum* (*Report of the Trustees for* 1885). Govt. Printer, Sydney, 17 pp. (p. 5)—list of Day's specimens, cases II and III.

CHAN, W. L. 1965. A systematic revision of the Indo-Pacific clupeoid fishes of the genus *Sardinella* (Family Clupeidae). *Jap. J. Ichthyol.*, **12** (3–6) : 104–118; *Ibid.*, **13** (1–3) : 1–39.

DAY, F. 1878. *The fishes of India, being a natural history of the fishes known to inhabit the seas and freshwaters of India, Burma, and Ceylon.* William Dawson & Sons, London, Pt IV, pp. i–xx, 553–778 and pls. 134–195.

—— 1883. *Great International Fisheries Exhibition, London,* 1883. *Catalogue of the exhibits in the Indian Section.* London, 198 pp. (list of Day's own specimens, pp. 176–197).

—— 1889. *The fauna of British India, including Ceylon and Burma. Fishes,* **1.** Taylor & Francis, London, 548 pp.

FOWLER, H. W. 1941. Contributions to the biology of the Philippine Archipelago and adjacent regions. *Bull. U.S. natn. Mus.*, **13** (100) : 1–879.

JENKINS, J. T. 1910. Notes on fish from India and Persia, with descriptions of new species. *Rec. Indian Mus.*, **5** : 123–140.

LLOYD, R. E. 1907. Notes on a collection of marketable fish from Akyab, with descriptions of a new species of *Lactarius*. *Rec. Indian Mus.*, **1** : 219–231.

MENON, A. G. K. & YAZDANI, G. M. 1963. Catalogue of type specimens in the Zoological Survey of India. *Rec. zool. Surv. India*, **61** : 91–190.

MOTWANI, M. P., JAYARAM, K. C. & SEHGAL, K. L. 1962. Fish and fisheries of Brahmaputra river system, Assam. *Trop. Ecol.*, **3** (1–2) : 17–43.

POLL, K., WHITEHEAD, P. J. P. & HOPSON, A. J. 1965. A new genus and species of clupeoid fish from West Africa. *Bull. Acad. r. Belg. Cl. Sci.*, (5) **51** : 277–292.

REGAN, C. T. 1917a. A revision of the clupeoid fishes of the genera *Sardinella, Harengula,* etc. *Ann. Mag. nat. Hist.*, (8) **19** : 377–395.

—— 1917b. A revision of the clupeoid fishes of the genera *Pomolobus, Brevoortia* and *Dorosoma* and their allies. *Ann. Mag. nat. Hist.*, (8) **19** : 297–316.

SRIVASTAVA, G. J. 1968. *Fishes of eastern Uttar Pradesh.* Vishwavidyalaya Prakashan, Varanasi, India, i–xxii, 1–163.

TALWAR, P. K. & CHAKRAPANY, S. (In press). Catalogue of the fishes figured in Day's *Fishes of India* and deposited in the Zoological Survey of India. *Rec. zool. Surv. India*

WHITEHEAD, P. J. P. 1962. A review of the Indo-Pacific gizzard shad genera *Nematalosa, Clupanodon* and *Konosirus* (Pisces: Dorosomatidae). *Bull. Br. Mus. nat. Hist.* (Zool.), **9** (2) : 87–102.

—— 1963. A revision of the recent round herrings (Pisces: Dussumieriidae). *Bull. Br. Mus. nat. Hist.* (Zool.), **10** (6) : 305–380.

—— 1965. A preliminary revision of the Indo-Pacific Alosinae (Pisces: Clupeidae). *Bull. Br. Mus. nat. Hist.* (Zool.), **12** (4) : 115–156.

—— 1967. The clupeoid fishes described by Lacepède, Cuvier and Valenciennes. *Bull. Br. Mus. nat. Hist.* (Zool.), Suppl. 2 : 1–180.

—— 1968. Indian Ocean anchovies collected by the *Anton Bruun* and *Te Vega*, 1963–64. *J. Mar. biol. Ass. India*, **9** (1) : 13–37.

—— 1970. The clupeoid fishes described by Steindachner. *Bull. Br. Mus. nat. Hist.* (Zool.), **20** (1) : 1–46.

—— (in press). A synopsis of the clupeoid fishes of India. *Symp. Indian Ocean Adj. Seas. Mar. biol. Ass. India.*

WHITEHEAD, P. J. P., BOESEMAN, M. & WHEELER, A. 1966. The types of Bleeker's Indo-Pacific elopoid and clupeoid species. *Zool. Verhandl. Leiden*, No. 84 : 1–152.

WHITLEY, G. P. 1958. *List of type specimens of recent fishes in the Australian Museum, Sydney.* (Unpublished typescript, 40 pp.)

ADDENDUM

In 1889 the Zoological Institute in Leningrad received a large collection of Day Fishes, comprising 357 specimens (284 species). These were a gift from the British Museum (Natural History), presumably taken from the large collection presented to the Museum just before Day's death. Amongst these specimens are 32 clupeoids, including a paralectotype of *Spratelloides malabaricus* (see p. 64), making a total of 19 clupeoid species.

P. K. Talwar, Ph.D.
Zoological Survey of India
34, Chittaranjan Avenue
Calcutta-12, India

P. J. P. Whitehead, B.A.
Department of Zoology
British Museum (Natural History)
Cromwell Road
London, SW7 5BD

PLATE 1

a. *Clupea sindensis, Fishes of India,* pl. 163 (2), F. Day del., 119 mm tot. l. (= *Sardinella sindensis*).

b. *Spratelloides malabaricus, Fishes of India,* pl. 161 (5), C. Achilles del. et lith., 69 mm tot. l (= *Dayella malabarica*).

c. *Clupea variegata, Fishes of India,* pl. 161 (4), C. Achilles del. et lith., 197 mm tot. l. (= *Gudusia variegata*).

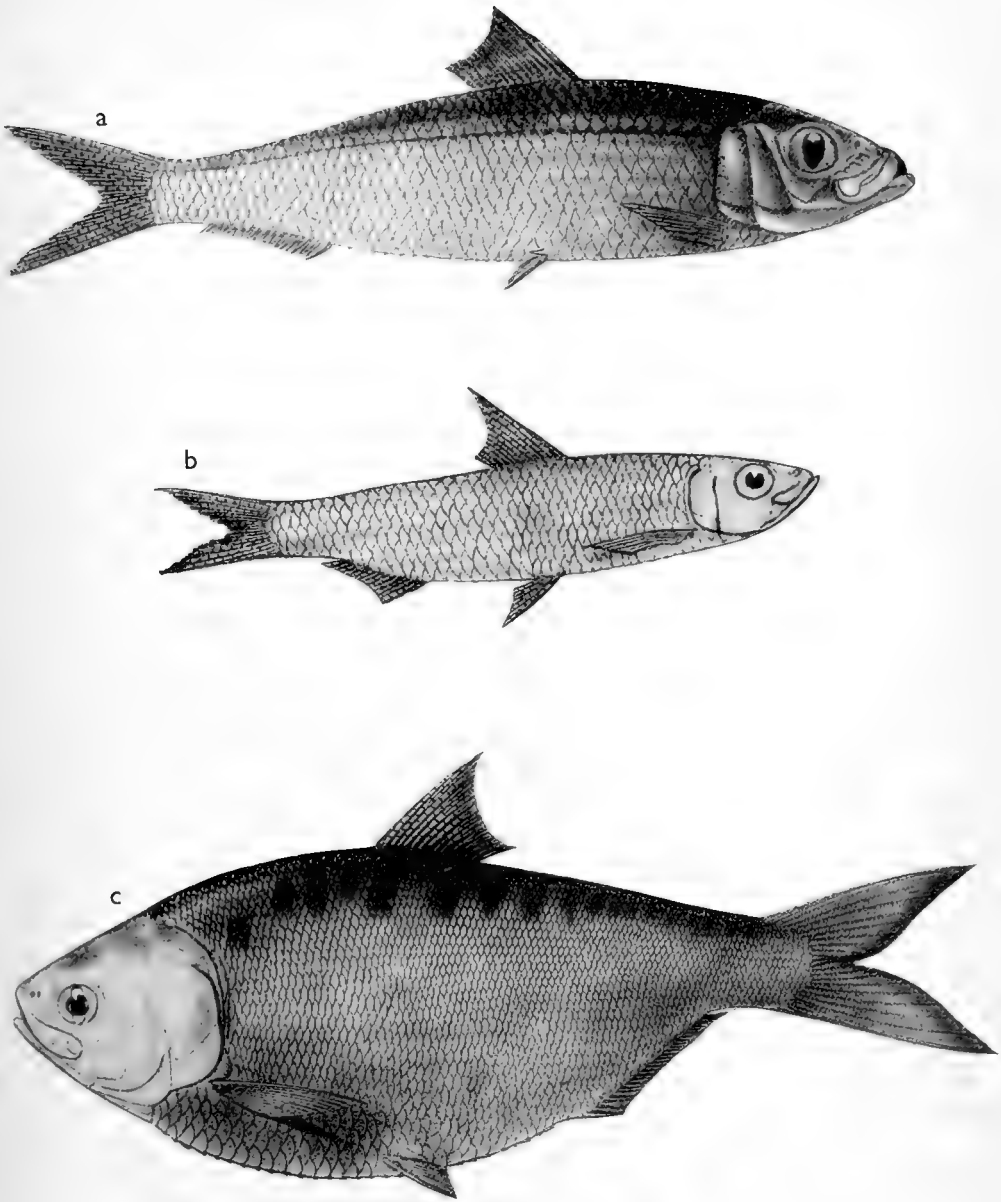
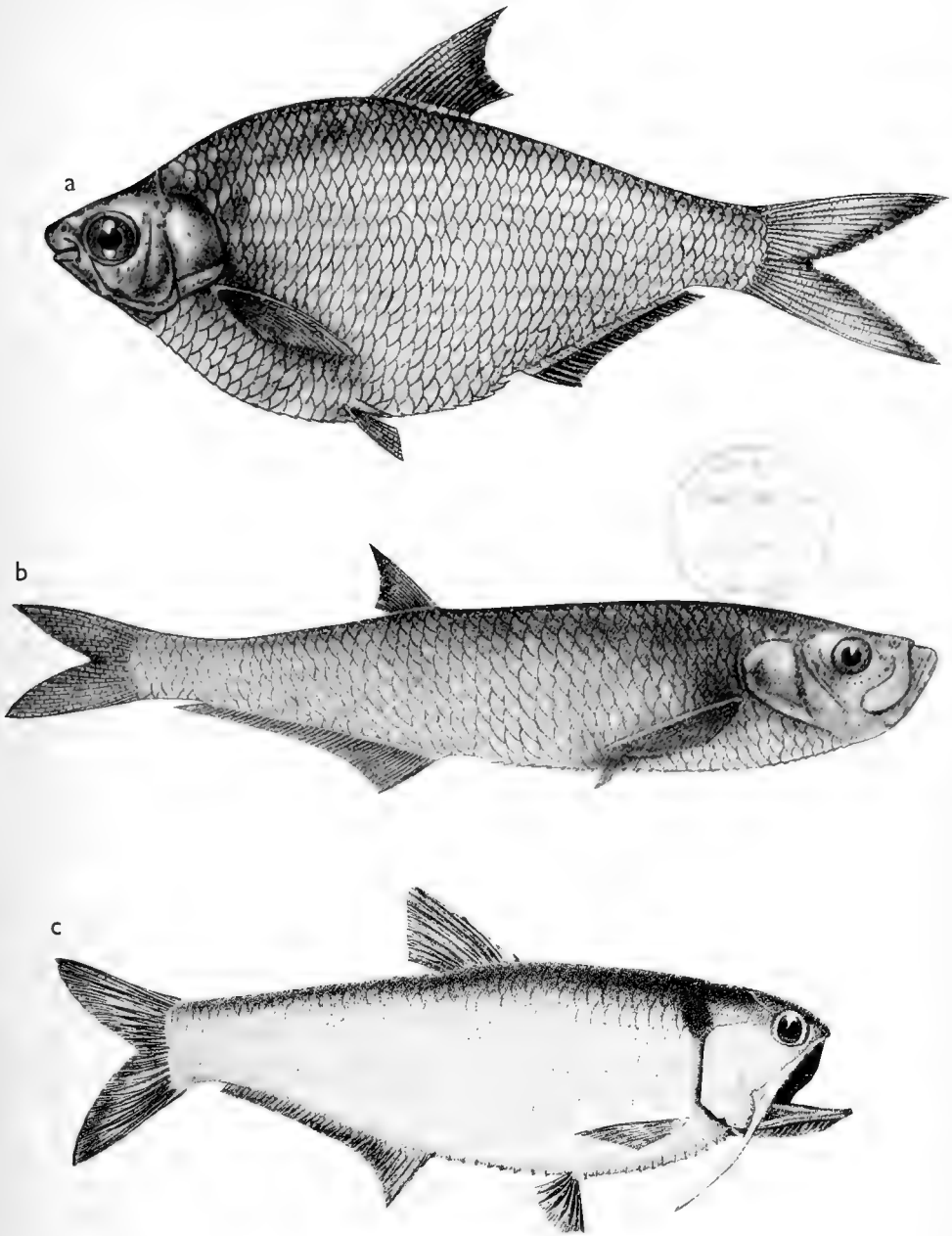

a
b
c

PLATE 2

a. *Chatoessus modestus*, *Fishes of India*, pl. 160 (1), C. Achilles del. et lith., 132 mm tot. l. (= *Gonialosa modesta*).

b. *Pellona sladeni*, *Fishes of India*, pl. 164 (1), F. Day del., 177 mm tot. l. (= *Ilisha sladeni*).

c. *Engraulis auratus*, *Fishes of Malabar*, pl. 19 (2), F. Day del. et sculp., 115 mm tot. l. (= *Thryssa dussumieri*).


a
b
c

A LIST OF SUPPLEMENTS TO THE ZOOLOGICAL SERIES OF THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY)

1. KAY, E. ALISON. Marine Molluscs in the Cuming Collection British Museum (Natural History) described by William Harper Pease. Pp. 96; 14 Plates. 1965. (Out of Print.) £3.75.
2. WHITEHEAD, P. J. P. The Clupeoid Fishes described by Lacepede, Cuvier and Valenciennes. Pp. 180; 11 Plates, 15 Text-figures. 1967. £4.
3. TAYLOR, J. D., KENNEDY, W. J. & HALL, A. The Shell Structure of Mineralogy at the Bivalvia. Introduction. Nuculacea-Trigonacea. Pp. 125; 29 Plates, 77 Text-figures. 1969. £4.50.
4. HAYNES, J. R. Cardigan Bay recent Foraminifera (Cruises of the R.V. *Antur*) 1962–1964. (*In press.*)

Printed in England by Staples Printers Limited at their Kettering, Northants, establishment

FINE STRUCTURE OF *BODO SALTANS* AND *BODO CAUDATUS* (ZOOMASTIGOPHORA : PROTOZOA) AND THEIR AFFINITIES WITH THE TRYPANOSOMATIDAE

B. E. BROOKER

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 22 No. 3
LONDON : 1971

FINE STRUCTURE OF *BODO SALTANS* AND *BODO CAUDATUS* (ZOOMASTIGOPHORA: PROTOZOA) AND THEIR AFFINITIES WITH THE TRYPANOSOMATIDAE

BY

BRIAN EDWARD BROOKER

Nuffield Institute of Comparative Medicine, London

Pp. 87–102; 6 *Plates*, 1 *Text-figure*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 22 No. 3
LONDON: 1971

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series, corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 22, *No.* 3 *of the Zoological series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation
Bull. Br. Mus. nat. Hist. (Zool.).

© Trustees of the British Museum (Natural History), 1971

TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 31 *December*, 1971 *Price* £1·20

FINE STRUCTURE OF *BODO SALTANS* AND *BODO CAUDATUS* (ZOOMASTIGOPHORA: PROTOZOA) AND THEIR AFFINITIES WITH THE TRYPANOSOMATIDAE

By B. E. BROOKER

CONTENTS

	Page
SYNOPSIS	89
INTRODUCTION	89
MATERIALS AND METHODS	90
RESULTS	90
Light microscopy	90
Bodo saltans	90
Bodo caudatus	92
Electron microscopy	92
Flagellar pocket	92
Basal bodies and flagella	92
Alimentary system	93
Microtubular systems	94
Kinetoplast-mitochondrion	95
Nucleus	96
Endocytoplasmic bacteria	96
Cytoplasmic membrane systems	96
DISCUSSION	97
ACKNOWLEDGEMENT	101
REFERENCES	101

SYNOPSIS

Characters specific to each of two species of *Bodo* are described for the first time. *Bodo saltans* possesses cytoplasmic bacteria, hair-like appendages (mastigonemes) on the anterior flagellum and circumbuccal lappets surrounding the opening of the alimentary system. In *B. caudatus*, an electron dense band separates the kinetoplast from the basal bodies of the flagella. In addition, clear differences exist between the microtubular systems associated with the buccal cavity and cytopharynx. It is suggested that the mastigonemes and circumbuccal lappets of *B. saltans* are responsible for the capture of food organisms.

In both species the alimentary system is a membrane-lined tube surrounded by a number of microtubules. The single mitochondrion is dilated in the vicinity of the basal bodies and contains a prominent kinetoplast. Since both these organelle systems closely resemble those found in members of the related Trypanosomatidae, the possible origin of this family from *Bodo* or a *Bodo*-like flagellate is discussed.

INTRODUCTION

Bodo is a cosmopolitan flagellate found in fresh and brackish waters and in some soils. This and other members of the Bodonidae are of interest chiefly because of their close relationship to the economically and medically important trypanosomes.

This relationship is based on the presence of a mass of DNA—the kinetoplast—situated in a dilatation of the single mitochondrion. In trypanosomes, this organelle has been regarded as a genetic system containing the information required for the synthesis of mitochondrial enzymes (Steinert, 1960) but in *Bodo* its function has not been examined. Of the many species of *Bodo* which have been described, *Bodo saltans* Ehrenberg, 1831 and *Bodo caudatus* Stein, 1878 are probably the two most commonly found. They occur in quite different habitats for whereas *B. caudatus* tends to be coprozoic, *B. saltans* is usually found in freshwater. Separation of the two species depends on such characters as body shape and size, length of the flagella and the position of the nucleus relative to that of the kinetoplast. However, the present fine structural study describes a number of clearly defined qualitative differences between *B. saltans* and *B. caudatus* which would not have been visible to the earlier light microscopists.

MATERIALS AND METHODS

Bodo saltans was isolated from a sample of fresh water taken from a pond near Slapton Ley, Devon. From this isolate, clone cultures were established on 0·1% w/v 'Oxoid' dehydrated liver infusion (pH 4·6) and maintained at 25°C.

Bodo caudatus was isolated from an infusion of pig faeces which was obtained from Winches Farm, near St. Albans, Hertfordshire. Clone cultures from this isolate were maintained at 25°C on 0·2% w/v 'Oxoid' beef extract (pH 5·8). In both cases, cultures were agnotobiotic. For light and electron microscopy, cultures were harvested after 3 days growth.

Light microscopy.—Phase contrast observations were made using a Leitz Ortholux microscope fitted with a Heine condenser. Flagellates were examined either alive or after fixation with 1% osmium tetroxide. Smears fixed in Schaudinn's fluid were stained with iron haematoxylin and examined by bright field microscopy.

Electron microscopy.—Flagellates were collected by centrifugation at 1,000 r.p.m. for 10 minutes and the resulting pellet fixed for 5 minutes at room temperature in 1% osmium tetroxide buffered to pH 7·4 either with 0·1 M Sorensen's phosphate buffer or 0·1 M veronal acetate (Michaelis). Before dehydration, the pellet was treated with 1% uranyl acetate in 25% ethanol for 30 minutes. After dehydration in ethanol-water mixtures and absolute ethanol, the pellet was treated with propylene oxide or toluene and embedded in Araldite. Sections were cut using a Porter-Blum MT2 ultramicrotome and stained in lead citrate prior to examination in an EM 6B electron microscope.

Some flagellates were fixed as before, washed in distilled water and dried onto grids. They were then placed in a coating unit and shadowed with gold/palladium at an angle of 30°. Negatively stained preparations were made using sodium phosphotungstate at pH 7·0.

RESULTS

LIGHT MICROSCOPY.—*Bodo saltans.*—The body of this flagellate is oval in shape (5–8 μm long and 2–5 μm wide) and has two flagella of unequal length which arise from the bottom of a depression (the reservoir or flagellar pocket) near the anterior

end of the cell (Fig. 1). During locomotion in which the body rotates on its own axis, the shorter anterior flagellum is extremely active while the posterior flagellum remains stationary or undergoes slight movement. When stationary, the flagellate often attaches itself to some object by the tip of its trailing flagellum and may then exhibit rapid oscillations. This behaviour is characteristic of *B. saltans*. The kinetoplast lies near to the basal bodies of the flagella and the nucleus, which con-

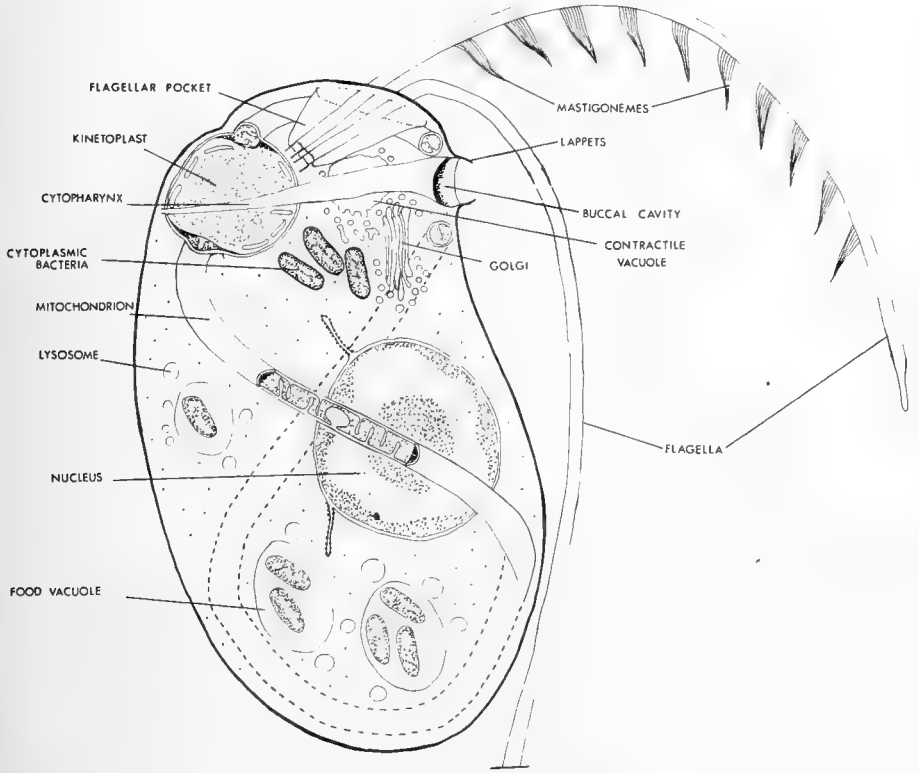


FIG. 1. Diagram of *Bodo saltans* showing the arrangement of the main organelles.

tains a conspicuous central karyosome, is central or mid-ventral in position. The single mitochondrion is markedly siderophilic and appears as a thin filament which originates from one side of the kinetoplast, describes a figure of eight or a loop within the cell and terminates at the opposite side of the kinetoplast. A single, round contractile vacuole appears at intervals at the anterior end of the living cell. It is situated just below and to one side of the flagellar pocket into which it periodically discharges its contents. The posterior half of the flagellate is occupied by a variable number of food vacuoles.

The opening of the alimentary system, the buccal cavity, is marked by a small vacuole on the ventral surface near the anterior end of the flagellate. Ingestion of bacteria is a very rapid process and can be observed satisfactorily only during the short periods of quiescence when it is attached to the substratum by its posterior flagellum. During ingestion, a bacterium is drawn into the buccal cavity and rapidly passes ventro-dorsally along a path which corresponds exactly with that of the cytopharynx (see later). A large vacuole then appears at a point which probably corresponds to the end of the cytopharynx and the bacterium passes into it. This food vacuole then slowly moves to the posterior end of the cell.

Bodo caudatus. When harvested in the logarithmic phase of growth, *B. caudatus* is long and narrow with a convex dorsal and concave ventral surface (8–14 μm long and 4–6 μm wide). The two flagella are of unequal length and arise from the bottom of the flagellar pocket near the anterior end of the cell. The anterior flagellum is the shorter but most active during locomotion. Situated in the anterior half of the cell, the nucleus frequently lies very close to the kinetoplast. As in *B. saltans*, the single mitochondrion is continuous at both its ends with the kinetoplast and describes a loop-like circuit of the cell. Almost the entire posterior half of the flagellate is occupied by food vacuoles and an active contractile vacuole lies close to the flagellar pocket. Although anteriorly a small buccal cavity is clearly visible, the ingestion of bacteria is very difficult to observe because of the relentless swimming habit of this flagellate.

Electron microscopy.—*Flagellar Pocket.* In both species of *Bodo*, the flagellar pocket is a lateral depression at the anterior end of the body. Because the two flagella emerge from the cell at the bottom of this structure (Fig. 1, Pl. 1, Fig. A), Pitelka (1961) referred to it as the circumflagellar depression. The flagellar pocket is lined with a unit membrane continuous with that covering the rest of the cell and below this, there lie a number of pellicular microtubules. Further details of these are given below.

Basal bodies and flagella. The two basal bodies are embedded in the cytoplasm at the base of the flagellar pocket and are therefore antero-lateral in position. They are structurally differentiated into 2 regions, an intracytoplasmic proximal portion and an extracytoplasmic transition zone which connects the intracytoplasmic portion to the flagellar shaft and is bounded by the flagellar membrane (Pl. 1, Fig. A). The proximal end of the basal bodies lies very close to the surface of the kinetoplast capsule (Pl. 1, Fig. A). The gap between these two structures is somewhat variable in width but is generally in the order of 100 nm and direct contact has never been observed. Under some conditions of fixation, a reticulum of fine filaments (8 nm wide) fills each basal body.

The junction of the basal body transition zone with the flagellum is marked by two transverse basal plates which are thickened peripherally (Pl. 1, Fig. B). The two central tubules of the axoneme originate just above the distal basal plate and the paraxial rod—a structure which runs parallel to the axoneme for about three quarters of its length—arises from a lateral extension of the proximal basal plate. The basal plate extensions of each flagellum face one another and the overlying flagellar

membranes are joined by a wide but very thin extracellular striated band (Pl. 1, Figs B and C). Of the three closely spaced striations, only the central one (5 nm wide) is prominent. Those lying on either side of it are more diffuse and can be satisfactorily resolved only in longitudinal sections of the band.

The transition zone of the basal bodies consists of 9 peripheral doublets of tubules each of which is joined to the adjacent flagellar membrane by a narrow connective. The intracytoplasmic portion is composed of 9 tubule triplets and is open proximally. The proximal ends of the basal bodies are connected by three striated rootlets (Pl. 1, Fig. D). Two of these arise from a single triplet on the basal body of the posterior flagellum and diverge slightly as they approach and insert onto the other basal body. A third rootlet running approximately parallel to the other two also connects the basal bodies. All three rootlets have a major period of 50 nm. The prominent bands delimiting the major repeating unit are 25 nm wide and between these lies a narrower 5 nm wide band. There is in addition, a 'Y' shaped rootlet which arises from the basal body of the anterior flagellum and passes antero-laterally to insert onto a group of 2–3 short microtubules running parallel to the cytopharynx (Pl. 1, Fig. D).

Both flagella contain the familiar '9+2' arrangement of tubules and a paraxial rod (Pl. 1, Fig. E). After running parallel to the axoneme for about three-quarters of its length, the paraxial rod tapers before terminating. Details of its structure are difficult to resolve but it appears to have a lattice-like architecture. The anterior flagellum of *Bodo saltans*, unlike that of *B. caudatus*, bears mastigonemes. These hair-like appendages are arranged in bundles along one side of the flagellum and have been reported elsewhere (Brooker, 1965). Metal-shadowed preparations of *B. saltans* show that the posterior flagellum bears a number of parallel transverse striations whose separation is 14 nm (Pl. 1, Fig. F). They are found only after the flagellum has emerged from the flagellar pocket and extend distally for a distance of 3 μm. In *B. caudatus* similar striations first appear at a level corresponding to the junction of the basal body with the flagellum but because they extend distally only for a distance of about 1 μm, they are not visible in shadowed material. In sectioned material, the striations are seen as periodic thickenings (14 nm wide) of both leaflets of the flagellar membrane (Pl. 1, Fig. E, Pl. 2, Fig. A). Such thickenings occupy about 25% of the circumference of the flagellar membrane (Pl. 1, Fig. E). On passing distally, this percentage gradually decreases so that in shadowed preparations of *B. saltans*, the array of striations appears to taper to an end (Pl. 1, Fig. F).

Alimentary system. The ingestion of food particles by *Bodo* takes place by way of permanent oral structures—the buccal cavity and cytopharynx—which lie to the right of the flagellar pocket (Pl. 2, Fig. B). The position at which the buccal cavity opens on to the surface of the cell differs in the two species. In *B. saltans*, it opens antero-ventrally (Pl. 2, Fig. C) but in *B. caudatus* it is found at the extreme anterior end of the flagellate (Pl. 2, Fig. D). Very rare sections in which a bacterium is found in the buccal cavity (Pl. 1, Fig. A) suggest that this organelle is capable of considerable distension. Frequently, the membrane lining the buccal cavity has a pronounced cell coat (Pl. 2, Fig. C) which takes the form of bundles of fine filaments projecting perpendicularly from the membrane. A number of structures, referred

to here as circumbuccal lappets, surround the opening of the buccal cavity of *B. saltans* (Pl. 2, Fig. B). They are flat, triangular projections (Pl. 3, Fig. A) which are joined at their bases to form a ring. Each lappet is composed of many fine filaments and arises from an intracellular band at the margin of the buccal cavity. These structures appear to be totally absent from *B. caudatus*.

From the left side of the buccal cavity arises an elongate tube lined by a unit membrane and surrounded by a number of microtubules (Pl. 2, Fig. B). In accordance with the terminology used for the oral apparatus of ciliates, this organelle will be referred to as the cytopharynx. In *Bodo saltans* the cytopharynx approaches the kinetoplast, passes underneath and to one side of it and on reaching the dorsal surface of the body, curves to one side (Pl. 3, Fig. C). In *B. caudatus*, it passes posteriorly just below the cell membrane (Pl. 2, Fig. D). Although the cytopharynx terminates just posterior to the kinetoplast, the microtubules associated with it frequently reach the posterior margin of the nucleus before terminating. In both species, the diameter of the lumen decreases distal to the buccal cavity. Numerous vesicles of variable diameter are always found underneath and to the right side of the cytopharynx in *B. saltans* (Pl. 2, Fig. B, Pl. 3, Fig. C). Although similar vesicles are occasionally found in *B. caudatus*, they are generally smaller and less numerous. Their origin is not clear, but many longitudinal sections of the cytopharynx suggest that they arise as invaginations of the cytopharyngeal membrane.

Both light and electron microscope observations suggest that ingestion of food particles takes place at the blind end of the cytopharynx. Since the diameter of the cytopharynx is at all points along its length smaller than that of food organisms found in the food vacuoles, ingestion must be accompanied by considerable distension of the cytopharynx. Ingestion results in the formation of a number of food vacuoles which migrate to the posterior half of the cell. The food vacuoles are bound by a single unit membrane and may contain one or more food organisms (Pl. 5, Fig. D). When digestion is complete, only a diffuse mass of undigestible material remains in the vacuole. Since such vacuoles do not accumulate in the cytoplasm, it seems likely that undigestible material is voided by the coalescence of the cell membrane with that of the food vacuole. However, this has never been observed.

Microtubular systems. Microtubules of external diameter 20–25 nm are associated with several organelles in the anterior half of the flagellate. Many, but not all, of the tubules which are associated with the flagellar pocket, cytopharynx and body, appear to arise from the proximal ends of the two basal bodies.

Bodo saltans. The microtubules which are to surround the cytopharynx pass along the flagellar pocket in two groups. At the opening of the flagellar pocket, three members of each group approach each other (Pl. 3, Fig. B) and continue as microtubule doublets. They curve over the narrow bridge of cytoplasm separating the flagellar pocket from the alimentary system and enter the walls of the buccal cavity where they adopt a 'U' shaped configuration. From the left side of this cavity, the microtubules follow the course of the cytopharynx and become arranged around it in two groups. Associated with the floor and left side of the cytopharynx is a group of 5 microtubules and with the roof a group of 3 (Pl. 3, Fig. D). The right

side of the organelle is free of tubules. The middle 3 tubules of the group of 5 are double and joined on their left side to the cytopharyngeal membrane by a short connective. Although 8 microtubules normally run parallel to the cytopharynx, 9 or 10 are sometimes found (Pl. 3, Fig. E). The microtubules of each group are connected by a number of fine filaments which occur at intervals (13 nm) along their length (Pl. 4, Fig. A). Beyond the blind end of the cytopharynx, the connectives of the microtubule doublets disappear but the arrangement of the two groups of tubules remains constant until they terminate near the dorsal surface of the flagellate.

Beneath the cell membrane at the anterior end of the cell lie a number of pellicular microtubules. Although some of these arise from the basal bodies of the flagella, many appear to have their origin near the opening of the flagellar pocket. From here, the microtubules spiral round the anterior end of the cell and on approaching the right side of the buccal cavity dip below the cell surface (Pl. 4, Fig. B). They then describe a semi-circular path as a curved band of 15–20 tubules (Pl. 4, Fig. C). Passing below the buccal cavity (Pl. 3, Fig. C) they move anteriorly and terminate in the cytoplasm between the cytopharynx and the flagellar pocket.

Bodo caudatus. The arrangement of microtubules associated with the buccal cavity resembles that described for *B. saltans.* The tubules which are to surround the alimentary system pass along the wall of the flagellar pocket and enter the buccal cavity. Here, transverse sections show that the tubules are arranged in a line along the left wall (Pl. 4, Fig. D, Pl. 5, Fig. A). As the tubules follow the cytopharynx from the left side of the buccal cavity, they distribute themselves around the cytopharyngeal membrane (Pl. 5, Fig. B) in 2 overlapping groups. One group associated with the roof of the cytopharynx usually contains 4 microtubules; the other group, which lies next to the floor and left side of the organelle, may contain 4, 5 or 6 tubules three of which are double and joined as in *B. saltans* to the cytopharyngeal membrane by a short connective. Such connectives disappear a short distance from the buccal cavity.

Another set of microtubules emerges from the flagellar pocket, spirals round the anterior end of the cell and comes to occupy the right hand wall of the buccal cavity just below the lining membrane (Pl. 4, Fig. D). The 15–20 microtubules in this set are joined by intertubular connectives and for most of their length travel posteriorly parallel to the buccal cavity and cytopharynx. A limb of the single mitochondrion which passes beneath the buccal cavity modifies the path taken by some of the tubules. As they travel posteriorly, the tubules gradually move away from the cytopharynx (Pl. 5, Figs A, B) and towards the cell membrane until, at a level beyond the blind end of the cytopharynx, they are seen as a row of pellicular microtubules. These tubules travel some distance posteriorly before terminating. In addition to this major set, an equally conspicuous row of very short parallel tubules is found on either side of the buccal cavity (Pl. 4, Fig. D).

Kinetoplast-mitochondrion.—Lying just below the cell membrane, the single mitochondrion describes a loop-like circuit of the cell (Fig. 1). In *Bodo saltans,* this organelle travels above and parallel to the cytopharynx, describes a semi-circular path around the right side of the buccal cavity (Pl. 5, Fig. D) and passes to the extreme posterior end of the cell before returning anteriorly to the basal body region.

The whole circuit of the mitochondrion frequently takes the form of a figure of eight. The form of the mitochondrion in *B. caudatus* is similar to that of *B. saltans* except that in the posterior region of the former it is frequently seen as a branching structure.

The cristae are predominantly plate-like and arise from the inner mitochondrial membrane. The granular matrix of the mitochondrion is dense but sometimes contains irregularly shaped bodies of much greater electron density (Pl. 5, Fig. C).

In the region of the basal bodies, a prominent spherical dilatation of the mitochondrial tube houses the kinetoplast. This will be referred to as the kinetoplast capsule. The kinetoplast is composed of a complex reticulum of fine filaments (2·5–3·0 nm thick) and contains a large number of irregularly distributed electron dense nodes (Pl. 6, Fig. A). It is separated from the wall of the mitochondrion by a number of cristae embedded in a thick layer of mitochondrial matrix (Pl. 6, Fig. A). The basal bodies of the flagella lie very close to the surface of the mitochondrial kinetoplast capsule but are never seen in contact with it. In *Bodo caudatus*, the basal bodies are separated from the capsule by a flat electron dense pad (Pl. 1, Fig. A).

Nucleus.—The relative position of the nucleus within the cell is one of the features by which the two species of *Bodo* may be separated. In *B. saltans* it is found mid-ventrally some distance from the kinetoplast capsule whilst in *B. caudatus*, it is always found very close to this part of the mitochondrion. The nucleus is bound by a nuclear envelope composed of two membranes of which the outer is continuous with the granular endoplasmic reticulum. A prominent and finely granular nucleolus of variable shape occupies the centre of the nucleus (Pl. 5, Fig. D). In *B. saltans* a layer of condensed chromatin is often seen attached to the inner membrane of the nuclear envelope but in *B. caudatus*, this component of the nucleus appears to be absent or at least is not visualized by the techniques used in this study.

Endocytoplasmic bacteria.—Structures have been observed in the cytoplasm of *Bodo saltans* which, on morphological grounds, have been tentatively identified as bacilliform bacteria (approximately 1 μm long and 0·3 μm wide). They are found in all individuals of the flagellate population and are always situated in the anterior half of the cell (Pl. 2, Fig. C, Pl. 4, Fig. C). Although the largest number of bacteria seen in one cell profile is four, the total population is probably much larger. They can be easily distinguished from food organisms since the latter are separated from the cytoplasm of the flagellate by the membrane of the food vacuole and are usually found at the posterior end of the cell (Pl. 5, Fig. D).

Each bacterial cell is bounded by a cell membrane 8 nm thick which bears on its outer surface a thin layer of filamentous material in direct contact with the host cytoplasm. Extensions of a layer of dense material lying beneath the cell membrane project into the electron lucent central portion of the bacterium which is traversed by fine fibrils. Deep, mid-length constrictions of the bacteria suggestive of division are commonly encountered and appear independently of the host cell division cycle (Pl. 6, Fig. C).

Cytoplasmic membrane systems.—The contractile vacuole is situated on the left side of the flagellate just below and to one side of the flagellar pocket (Pl. 4, Fig. D). Surrounding the vacuole is a number of vesicles and tubules which serial sections

show to be continuous with the lumen of the vacuole (Pl. 6, Fig. B). After systole, the membrane lining the vacuole appears rounded in section. At discharge, the membranes between the flagellar pocket and contractile vacuole coalesce and the contents of the vacuole are discharged into the flagellar pocket. The thin layer of cytoplasm between the membranes of the flagellar pocket and contractile vacuole is traversed by a number of concentrically arranged circular septa. Coated vesicles are commonly encountered in the vicinity of the vacuole and often they are seen with their membrane confluent with that of the vacuole.

The Golgi apparatus is situated directly below the cytopharynx (Pl. 4, Fig. C, Pl. 5, Fig. D) and to the right side of the contractile vacuole and is composed of a stack of 6–10 compressed saccules. Although vesicles of both the smooth and coated type are actively proliferated from the margins of all the Golgi saccules, there is frequently a notable concentration in the region of the distal saccule.

Cisternae of granular endoplasmic reticulum arise from the outer membrane of the nuclear envelope and ramify throughout the cell. One limb of this reticulum is permanently associated with the posterior margin of the cytopharynx and runs parallel to it for most of its length (Pl. 3, Fig. D).

DISCUSSION

Since, at the level of the light microscope, *Bodo saltans* and *B. caudatus* appear to possess the same major organelle systems, separation of the two species is based on differences in the spatial arrangement of these organelles and on differences in the size and shape of the body. Whilst confirming the validity of such criteria, the present study has shown that separation is also possible using characters which are beyond the resolution of the light microscope. Thus in *B. saltans*, circumbuccal lappets, endocytoplasmic bacteria and mastigonemes on the anterior flagellum are consistently present but are never found in *B. caudatus*. Similarly, the dense layer of material which separates the basal bodies of the flagella from the kinetoplast capsule is present only in *B. caudatus*. Although Pitelka (1961) was only able to make a tentative identification of the flagellate she studied, it is clear that it was *B. saltans* for her pictures show the cytoplasmic bacteria and circumbuccal lappets of this species.

The alimentary system and the microtubules associated with it have been briefly reported by Pitelka (1961). She pointed out that the non-contractile rostral vacuole described by Hollande (1942) corresponded to the cup-like depression at the opening of the alimentary system, a structure which has been referred to as the buccal cavity in the present study. Sections of the alimentary system containing partially ingested bacteria suggest that the buccal cavity and cytopharynx are capable of considerable distension. This conclusion is supported by the observations made by Sinton (1912) on a flagellate which he referred to as *Prowazekia urinaria* but which, from his description, was probably *Bodo caudatus*. He observed that the flagellate was able to ingest not only large bacteria but also red blood cells and that on these occasions the buccal cavity was capable of being greatly distended. As Sinton describes it, the path taken by the bacteria through the cell during ingestion

corresponds exactly to the course of the cytopharynx described in the present study. A similar conclusion has been drawn from the light microscope observations of feeding in *B. saltans*. These results are contrary to Pitelka's assertion that bacteria do not pass along the cytopharynx. Although the function of the microtubules associated with the alimentary system is unknown, it is possible that they confer a degree of elasticity on the organelle which enables it to return to its normal shape and size once ingestion is complete. Schuster (1968) suggested a similar function for the cytopharyngeal tubules of the cryptomonad flagellate *Cyathomonas truncata* and extended this proposal to the case of *Bodo*.

The capture of prey by Bodo *caudatus* has been described by Sinton (1912). According to this author, the distal portion of the anterior flagellum is capable of grasping bacteria and propelling them to the opening of the buccal cavity by coiling movements. Infolding movements of the edges of the buccal cavity then initiate ingestion. This mechanism is possible in *B. caudatus* only because the buccal cavity opens anteriorly and is therefore ideally situated to receive bacteria carried to it by the anterior flagellum. Because the buccal cavity of *B. saltans* opens anteroventrally, the mechanism described above for *B. caudatus* does not appear adequate to explain the capture of food organisms. Instead, a mechanism involving the mastigonemes of the anterior flagellum is proposed. Although the mastigonemes do not appear to play a major role in locomotion (Holwill, 1966), it is possible that during the oar-like movements of the anterior flagellum (Holwill, 1966) they exert a component force in the direction of the buccal cavity which sweeps food organisms towards it. Such a mechanism may bring bacteria to the vicity of the buccal cavity but the initiation of ingestion probably depends on movements of the margins of the buccal cavity as described by Sinton (1912) for *B. caudatus*. In this process, participation by the circumbuccal lappets may be important. It is visualized therefore that the mastigonemes and the circumbuccal lappets are functionally integrated to form a system responsible for the capture and ingestion of food organisms. Schuster (1968) has described a filamentous fringe surrounding the opening of the cytopharynx of *Cyathomonas* which, like the circumbuccal lappets of *B. saltans*, has its origin beneath the cell membrane and is believed to assist in feeding.

In her study of *Bodo saltans*, Pitelka (1961) suggested that the cytopharynx was a modified intracytoplasmic flagellum. This suggestion was based on the observation that the cytopharynx is surrounded by 9 microtubules and arises close to the surface of the kinetoplast near the basal bodies of the flagella. However, it has been shown here that the cytopharynx passes beyond the kinetoplast capsule and although occasionally surrounded by 9 or 10 tubules, 8 is the usual number. In view of these findings, the homology attempted by Pitelka must be considered doubtful.

Vesicles of various sizes are associated with the cytopharynx of *Bodo* (Pitelka, 1961), *Ichthyobodo(Costia)necator* (Joyon and Lom 1966, 1969) and *Cyathomonas truncata* (Mignot, 1965; Schuster, 1968). In the case of *Cyathomonas*, Mignot (1965) believed that these vesicles arise from the Golgi apparatus and Schuster (1968) has suggested that they contain digestive enzymes which are ultimately emptied into the food vacuoles. In *Bodo* however, profiles showing an undulatory cytopharyngeal

membrane strongly suggest that the vesicles arise by pinocytosis although in the absence of tracer experiments this can only be conjecture.

Although in most respects the flagella of *Bodo* closely resemble those described from other kinetoplastid flagellates (Pyne, 1960; Anderson and Ellis, 1965; Vickerman, 1969), they do possess two features, namely the striations of the posterior flagellum and the extracellular interflagellar connective, which are not shared by other members of this group. The significance of these structures is not known, but an extracellular connection between the 2 flagella may go some way to explaining synchrony of these organelles during movement. The paraxial rod of both flagella arises from the proximal basal plate but in the closely related trypanosomatids it only becomes recognizable a short way along the flagellum.

The mitochondrion was probably first visualized by Whitmore (1911) who described a fibril from *Bodo asiaticus* (= *B. caudatus*) which ran from the kinetoplast to the posterior end of the cell. Alexeieff (1912) observed this '*fibrille sidérophile*' in *B. caudatus* and *B. edax* but reported that it could only be seen in flagellates from young cultures. A detailed study of this structure was made by Hollande (1936, 1942). He noted that it was a constant feature of all species of *Bodo* but that there was a species difference in the extent to which it was developed. Because the '*côte*' or '*cordon siderophile*', as Hollande called it, was best developed in *B. saltans*, he paid more attention to this species and described in some detail the path taken by it through the cell. As noted by Pitelka (1961), it seems probable that Hollande was describing the mitochondrion since electron microscopy shows that this is the only organelle which follows an identical path through the cell.

The enclosure of the DNA-containing kinetoplast in a dilatation of the mitochondrial tube is a feature uniting *Bodo* with members of the Trypanosomatidae. However, they differ in the organization of the kinetoplast for whereas in the Trypanosomatidae the kinetoplast is disk shaped with its component fibrils arranged antero-posteriorly, in *Bodo* it is spherical with its fibrils forming a reticulum. Although in all kinetoplastid flagellates the basal bodies of the flagella lie very close to the surface of the kinetoplast capsule, no physical connection between the two has been found. Such a connection has been sought because in many trypanosomatids the two structures are linked in morphogenesis and appear connected after cell rupture (Simpson, 1968). The present study suggests that in the case of *Bodo caudatus* no direct connection is possible because the two structures are separated by a thick electron dense pad. The observations made by Simpson (1968) on *Leishmania tarentolae* led him to suggest that the kinetoplast capsule is attached to the basal body by an EDTA-sensitive cytoplasmic cement. There seems no reason why this explanation cannot be extended to other kinetoplastid flagellates.

Electron dense bodies similar to those found in the matrix of the mitochondrion have also been described from *Crithidia fasciculata* (Brooker, 1971) and in *Tetrahymena pyriformis* Levy and Elliott (1968) found that they become more numerous when the ciliates are starved. Although their significance is unknown, it is interesting that these bodies resemble the altered kinetoplast DNA of trypanosomatid flagellates which have been exposed to acriflavine (Kusel, Moore and Weber, 1967; Hill and Anderson, 1969). Although dyskinetoplastic *Bodo caudatus* was obtained

by Robertson (1929) using acriflavine, the electron miscroscopy of the kinetoplast after this treatment has not been studied.

The endocytoplasmic bacteria of *Bodo saltans* appear to be a constant feature of this species. Profiles showing constrictions across the equator of some bacteria support the assumption that they multiply to keep pace with division of the flagellate. Gram stained preparations of *B. saltans* provide little useful information since it is difficult to distinguish endocytoplasmic bacteria from food organisms. However, since the walls of Gram negative bacteria are very thin (Kellenberger and Ryter, 1958) compared with those of Gram positive bacteria (Glauert, 1962) the cytoplasmic bacteria of *Bodo* are judged to be Gram negative.

Bodies thought to be bacteria constantly occur in or on many species of protozoa as shown by the review of Kirby (1941). In most cases their identity and function is unknown. Since, in the case of *Bodo saltans*, there is no evidence to suggest that the flagellate benefits or is harmed by the association it is impossible at this stage to decide whether the bacteria are parasitic or symbiotic. However, in another kinetoplastid flagellate, namely *Crithidia oncopelti*, cytoplasmic bacteria or 'polar bodies' have been described by Newton and Horne (1957) which appear to provide the flagellate with lysine (Gill and Vogel, 1962).

Although there now appears to be general acceptance of the theory which holds that trypanosomes originated from the intestinal flagellates of insects (Hoare, 1948; Baker, 1963), the origins of the family still seem unclear. The presence in all trypanosomatid flagellates of a barren basal body in addition to that which produces the single motile flagellum (Rudzinska and Vickerman, 1969) may indicate origin from a biflagellate ancestor. Since at some stage this is likely to have been a free living flagellate, possible descent from *Bodo* or a *Bodo*-like organism is worth a brief consideration. Although the kinetoplast-mitochondrion is an obvious character uniting both groups of flagellates, it appears that an organelle comparable to the cytopharynx of *Bodo* has also been retained in a more or less modified form by many trypanosomatids (Brooker, 1971). In trypanosomatids, it is a deep (cytopharynx) or shallow (cytostome) invagination of the cell membrane associated, as in *Bodo*, with a number of microtubules. In both cases this organelle is endocytotic but whereas in *Bodo* it is primarily concerned with the ingestion of bacteria, in those trypanosomatids which have been examined it appears to be pinocytotic (Steinert and Novikoff, 1960; Preston, 1969; Brooker, 1971). Qualitative and quantitative differences in the nature of food ingested by *Bodo* and trypanosomatids may go some way to explain observed differences both in cell shape and the spatial arrangement of some organelles. Thus, the cytopharynx of *Bodo*, unlike that of trypanosomatids, is situated some distance from the flagellar pocket in order to facilitate prey capture and virtually the entire posterior half of the cell is devoted to the accommodation of food vacuoles. It is proposed therefore that the adoption of a parasitic mode of life by a *Bodo*-like flagellate and the subsequent abandonment of bacterophagic nutrition could have produced changes in body form which, together with other physiological adaptations led to the emergence of an ancestral trypanosomatid. Although such changes would have resulted in the retention of the cytopharynx, it

is assumed that the loss of one flagellum and development of the relatively sparse microtubular system occurred at some later stage.

ACKNOWLEDGEMENTS

I gratefully acknowledge the technical assistance given by Mr. C. G. Ogden who was responsible for many of the electron micrographs used in this paper.

KEY TO ABBREVIATIONS USED IN THE PLATES

ax	axoneme	G	Golgi apparatus
b	bacterium	ger	granular endoplasmic reticulum
bb	basal body	ifc	interflagellar connective
bc	buccal cavity	k	kinetoplast
cb	cytoplasmic bacterium	m	mitochondrion
cbl	circumbuccal lappets	mast	mastigonemes
cv	contractile vacuole	mt	microtubule
cyt	cytopharynx	n	nucleus
f	flagellum	pr	paraxial rod
fp	flagellar pocket	rt	rootlet
fv	food vacuole	ves	vesicle

REFERENCES

ALEXEIEFF, A. 1912. Sur la revision du genre *Bodo* Ehrbg. Arch. Protistenk. **26** : 413–419.

ANDERSON, W. A. & ELLIS, R. A. 1965. Ultrastructure of *Trypanosoma lewisi*: flagellum, microtubules and the kinetoplast. *J. Protozool.* **12** : 483–499.

BAKER, J. R. 1963. Speculations on the evolution of the family Trypanosomatidae Doflein, 1901. *Expl. Parasit.* **13** : 219–233.

BROOKER, B. E. 1965. Mastigonemes in a bodonid flagellate. *Expl. Cell Res.* **37** : 300–305

—— 1971. The fine structure of *Crithidia fasciculata* with special reference to the organelles involved in the ingestion and digestion of protein. *Z. Zellforsch.* **116** : 532–563.

GILL, J. W. & VOGEL, H. J. 1962. Lysine synthesis and phylogeny: biochemical evidence for a bacterial-type endosymbiote in the protozoon *Herpetomonas* (*Strigomonas*) *oncopelti*. *Biochim. biophys. Acta* **56** : 200–201.

GLAUERT, A. M. 1962. Fine structure of bacteria. *Br. med. Bull.* **18** : 245–250.

HILL, G. C. & ANDERSON, W. A. 1969. Effects of acriflavine on the mitochondria and kinetoplast of *Crithidia fasciculata*. Correlation of fine structural changes with decreased mitochondrial enzyme activity. *J. Cell Biol.* **41** : 547–561.

HOARE, C. A. 1948. The relationship of the haemoflagellates. In Proceedings of Fourth International Congress of Tropical Medicine. **2** : 1110–1116.

HOLLANDE, A. 1936. Sur la cytologie d'un flagellé du genre *Bodo*. *C.r. Séanc. Biol.* **123** : 651–653.

—— 1942. Étude cytologique et biologique de quelques flagellés libres. *Archs. Zool. exp. gén.* **83** : 1–268.

HOLWILL, M. E. J. 1966. Physical aspects of flagellar movement. *Physiol. Rev.* **46** : 696–785.

JOYON, L. & LOM, J. 1966. Sur l'ultrastructure de *Costia necatrix* Leclercq (Zoofiagellé); place systématique de ce Protiste. *C.r. Acad. Sci.* (*Paris*) **262** : 660–663.

—— —— 1969. Étude cytologique, systématique et pathologique d'*Ichtyobodo necator* (Henneguy, 1883) Pinto, 1928 (Zooflagelle). *J. Protozool.* **16** : 703–719.

KELLENBERGER, E. & RYTER, A. 1958. Cell wall and cytoplasmic membrane of *Escherichia coli*. *J. biophys. biochem. Cytol.* **4** : 323–326.

Kirby, H. W. 1941. In Protozoa in Biological Research. Eds. Calkins, G. N. and Summers, F. N. New York.

Kusel, J. P., Moore, K. E. & Weber, M. M. 1967. The ultrastructure of *Crithidia fasciculata* and morphological changes induced by growth in acriflavin. *J. Protozool.* **14** : 283–296.

Levy, M. R. & Elliott, A. M. 1968. Biochemical and ultrastructural changes in *Tetrahymena pyriformis* during starvation. *J. Protozool.* **15** : 208–222.

Mignot, J. P. 1965. Etude ultrastructurale de *Cyathomonas truncata* From. (Flagellé Cryptomonadine). *J. Microscopie* **4** : 239–252.

Newton, B. A. & Horne, R. W. 1957. Intracellular structures in *Strigomonas oncopelti* 1. Cytoplasmic structures containing ribonucleoprotein. *Expl. Cell. Res.* **13** : 563–574.

Pitelka, D. R. 1961. Observations on the kinetoplast-mitochondrion and the cytostome of *Bodo*. *Expl. Cell Res.* **25** : 87–93.

Preston, T. M. 1969. The form and function of the cytostome-cytopharynx of the culture forms of the elasmobranch haemoflagellate *Trypanosoma raiae* Laveran and Mesnil. *J. Protozool.* **16** : 320–333.

Pyne, C. K. 1960. L'ultrastructure de l'appareil basal des flagelles chez *Cryptobia helicis* (Flagellé, Bobonidae). *C.r. Acad. Sci. (Paris)* **250** : 1912–1914.

Robertson, M. 1929. The action of acriflavine upon *Bodo caudatus*. *Parasitology* **21** : 375–416.

Rudzinska, M. A. & Vickerman, K. 1969. The fine structure. In Infectious blood diseases of man and animals. *New York* **1** : 217–306.

Schuster, F. L. 1968. The gullet and trichocysts of *Cyathomonas truncata*. *Expl. Cell Res* **49** : 277–284.

Simpson, L. 1968. Behaviour of the kinetoplast in *Leishmania tarentolae* on cell rupture. *J. Protozool.* **15** : 132–136.

Sinton, J. A. 1912. Some observations on the morphology and biology of *Prowazekia urinaria* (*Bodo urinarius*, Hassall). *Ann. trop. Med. Parasit.* **6** : 245–269.

Steinert, M. 1960. Mitochondria associated with the kinetonucleus of *Trypanosoma mega*. *J. biophys. biochem. Cytol.* **8** : 542–546.

Steinert, M. & Novikoff, A. B. 1960. The existence of a cytostome and the occurrence of pinocytosis in the trypanosome *Trypanosoma mega*. *J. biophys. biochem. Cytol.* **8** : 563–569.

Vickerman, K. 1969. The fine structure of *Trypanosoma congolense* in its bloodstream phase. *J. Protozool.* **16** : 54–69.

Whitmore, E. 1911. *Prowazekia asiatica* (syn. *Bodo asiaticus* Castellani and Chalmers). *Arch. Protistenk.* **22** : 370–378.

B. E. Brooker
Nuffield Institute of Comparative Medicine
The Zoological Society of London
Regent's Park
London, N.W.1

PLATE 1

FIG. A. Longitudinal section through the anterior end of *B. caudatus*. The buccal cavity is seen in transverse section. A bacterium in an early stage of ingestion occupies the greatly distended buccal cavity Note the dense pad (arrowheads) lying between the basal body of the flagellum and the kinetoplast capsule. × 29,500.

FIG. B. Longitudinal section through the basal plate region of two flagella showing the striated interflagellar connective. × 96,000.

FIG. C. Transverse section of two flagella at the level of the basal plates which are joined by the interflagellar connective. × 54,000.

FIG. D. Transverse section of the basal bodies of *B. saltans*. They are connected by striated rootlets. The rootlet passing from the basal body of the anterior flagellum to the vicinity of the cytopharynx can just be seen (arrow). This cell is in the early stages of division and the daughter basal bodies are already forming. A rootlet connects the basal body of the anterior flagellum with its daughter. × 56,500.

FIG. E. Transverse section of the posterior flagellum of *B. caudatus* showing the axoneme and the paraxial rod. On one side, a flagellar striation is seen as a thickening of the flagellar membrane associated with sub-membrane material. × 56,500.

FIG. F. Posterior flagellum of *B. saltans* showing the parallel striations. Metal shadowed. × 44,500.

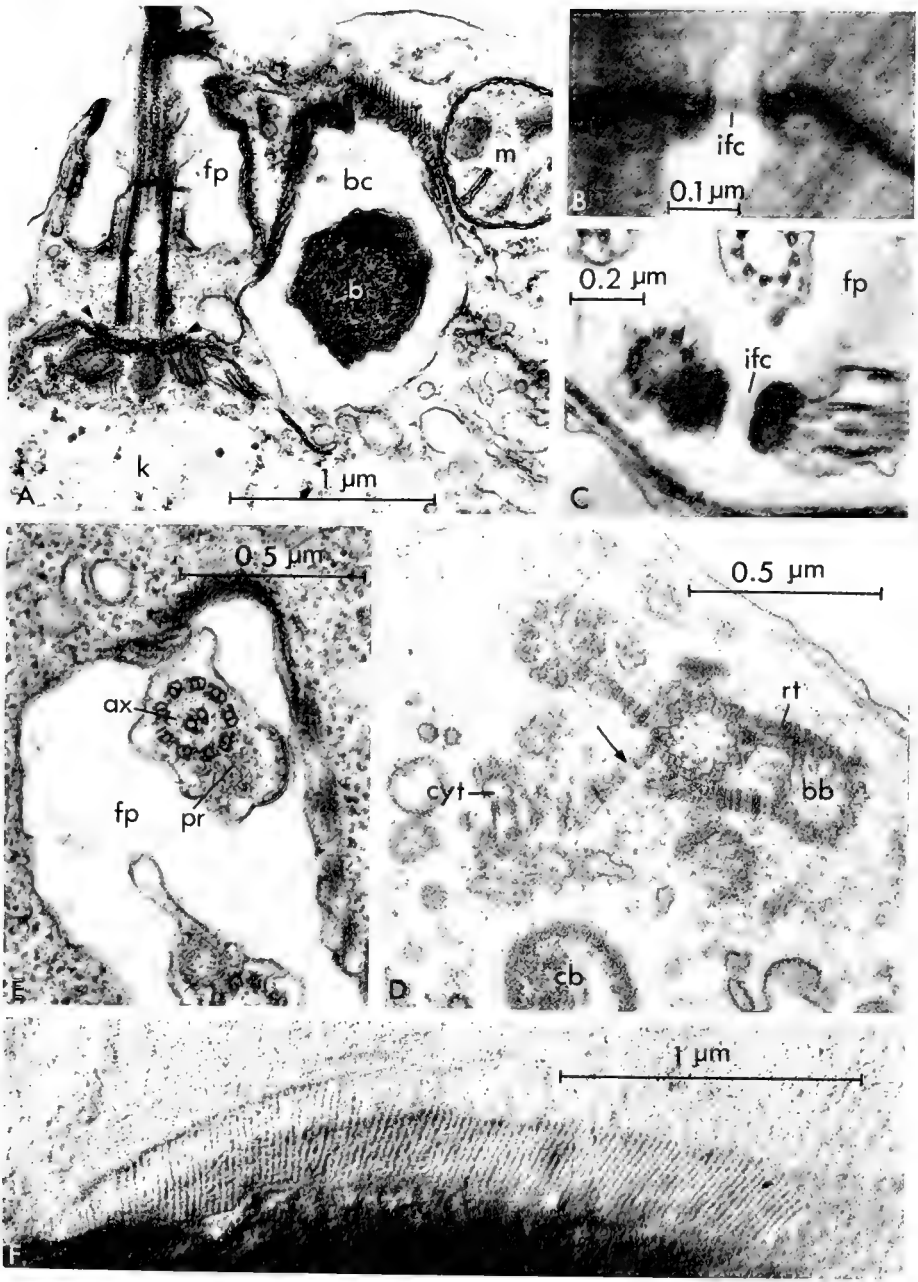

fp
bc
m
b
k
1 μm
A
ifc
0.1 μm
B
0.2 μm
fp
ifc
C
0.5 μm
ax
fp
pr
E
0.5 μm
rt
cyt
bb
cb
D
1 μm
F

PLATE 2

FIG. A. Longitudinal section through the posterior flagellum of *B. caudatus* showing the striations of the flagellar membrane. × 56,500

FIG. B. Transverse section through *B. saltans* showing the relationship of cytopharynx to the flagellar pocket. Small portions of the circumbuccal lappets are visible. One of the basal body rootlets appears clearly. Note the abundant vesicles lying on one side of the cytopharynx. × 29,500

FIG. C. Longitudinal section of the buccal cavity and part of the cytopharynx of *B. saltans*. Note the pronounced cell coat (arrowheads) of the buccal cavity membrane, the cytoplasmic bacteria and position of the lappets. The anterior end of the flagellate is at the top of the micrograph. × 30,000

FIG. D. Longitudinal section of *B. caudatus* showing the anteriorly directed buccal cavity. The kinetoplast and nucleus lie very close to each other in this species. The anterior end of the flagellate is to the right of the micrograph. × 22,000.

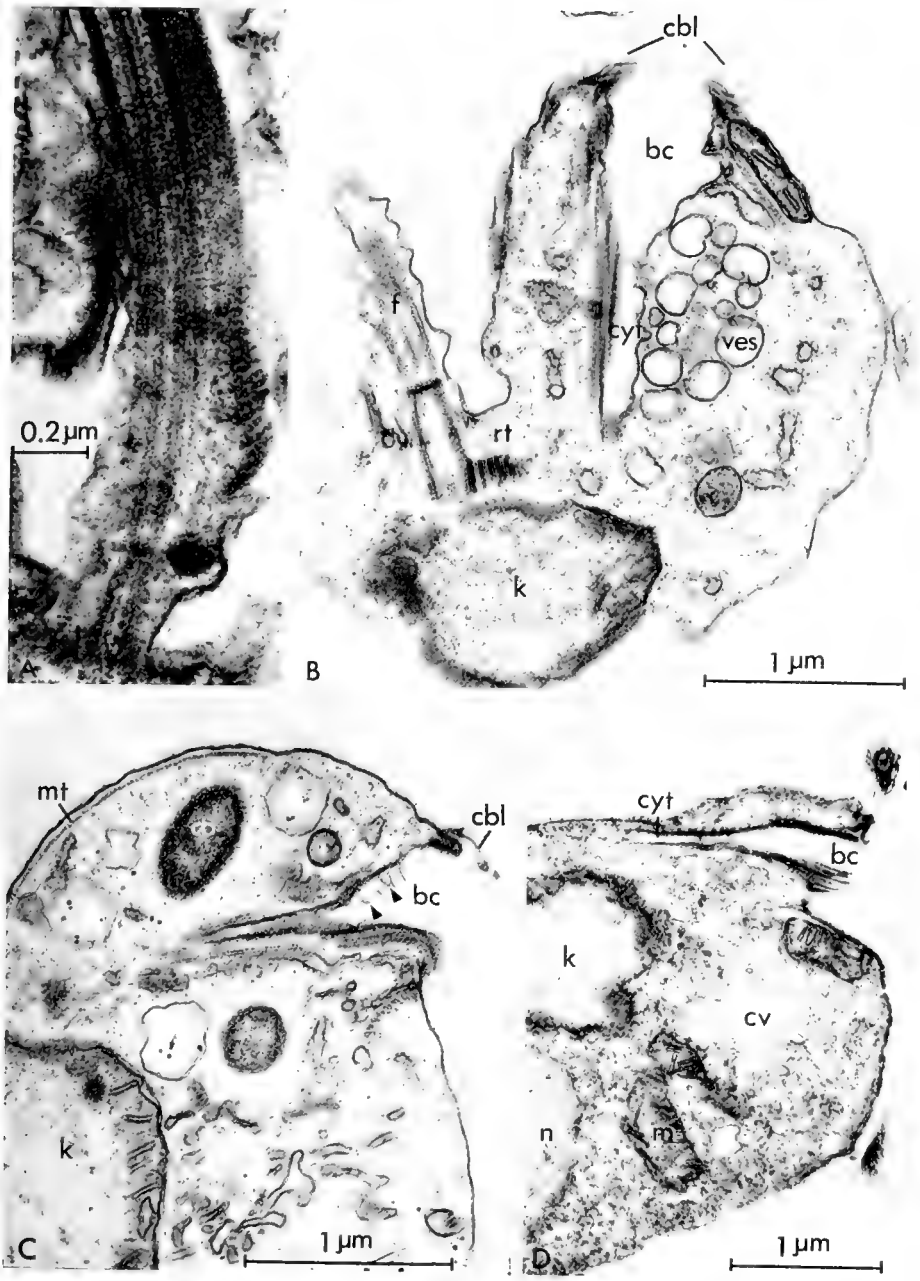

0.2 µm
A
cbl
bc
f
cyt
ves
rt
k
B
1 µm
mt
cbl
bc
k
C
1 µm
cyt
bc
k
cv
n
m
D
1 µm

PLATE 3

FIG. A. Negatively stained *B. saltans* showing the position of the circumbuccal lappets relative to the mastigonemes of the anterior flagellum. The position of the flagellum here corresponds to the bottom of the effective stroke. × 28,500.

FIG. B. Section through the flagellar pocket of *B. saltans* demonstrating the pairing of microtubules shortly before they enter the buccal cavity. × 37,500.

FIG. C. Longitudinal section of *B. saltans* showing the undulatory path of the cytopharynx. The Golgi apparatus lies directly beneath this organelle. Note the numerous vesicles associated with the cytopharynx and the undulation of the cytopharyngeal membrane. A band of microtubules circumscribes the floor of the buccal cavity. × 45,000

FIG. D. Transverse section of the cytopharynx of *B. saltans* showing eight microtubules of which three are paired. Note the vesicles lying beside it. × 66,000

FIG. E. Transverse section of the cytopharynx of *B. saltans* showing that it is occasionally surrounded by nine microtubules. × 40,000

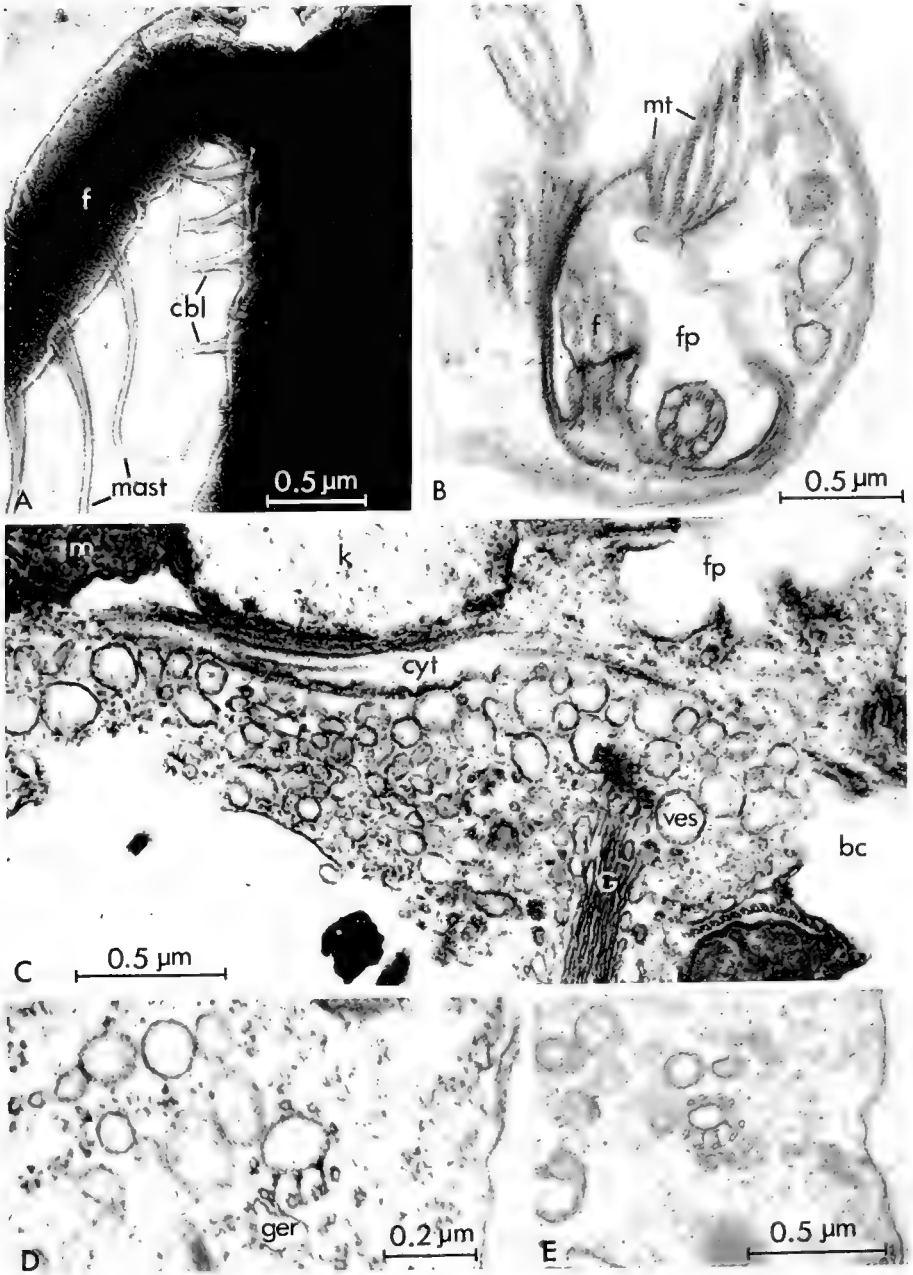

f
cbl
mast
A
0.5 µm
mt
f
fp
B
0.5 µm
m
k
fp
cyt
ves
bc
C
0.5 µm
ger
D
0.2 µm
E
0.5 µm

PLATE 4

FIG. A. Tangential section of the cytopharynx in *B. saltans*. Note the connectives joining adjacent tubule pairs. × 56,700.

FIG. B. Longitudinal section of *B. saltans* which passes through the flagellar pocket and cytopharynx transversely. The microtubule dipping below the surface of the cell is one of many which eventually pass under the buccal cavity as shown in Fig. C. Note the position of the cytopharynx and the vesicles lying one one side of it. × 30,000.

FIG. C. Transverse section of the buccal cavity of *B. saltans*. Note the tract of microtubules passing under the floor of this organelle. × 30,000.

FIG. D. Longitudinal section of *B. caudatus* which passes through the buccal cavity and flagellar pocket transversely. The contractile vacuole lies next to the flagellar pocket. Microtubules destined to surround the cytopharynx are arranged in a row in this section. Note the row of tubules associated with the opposite wall of the buccal cavity. × 40,000

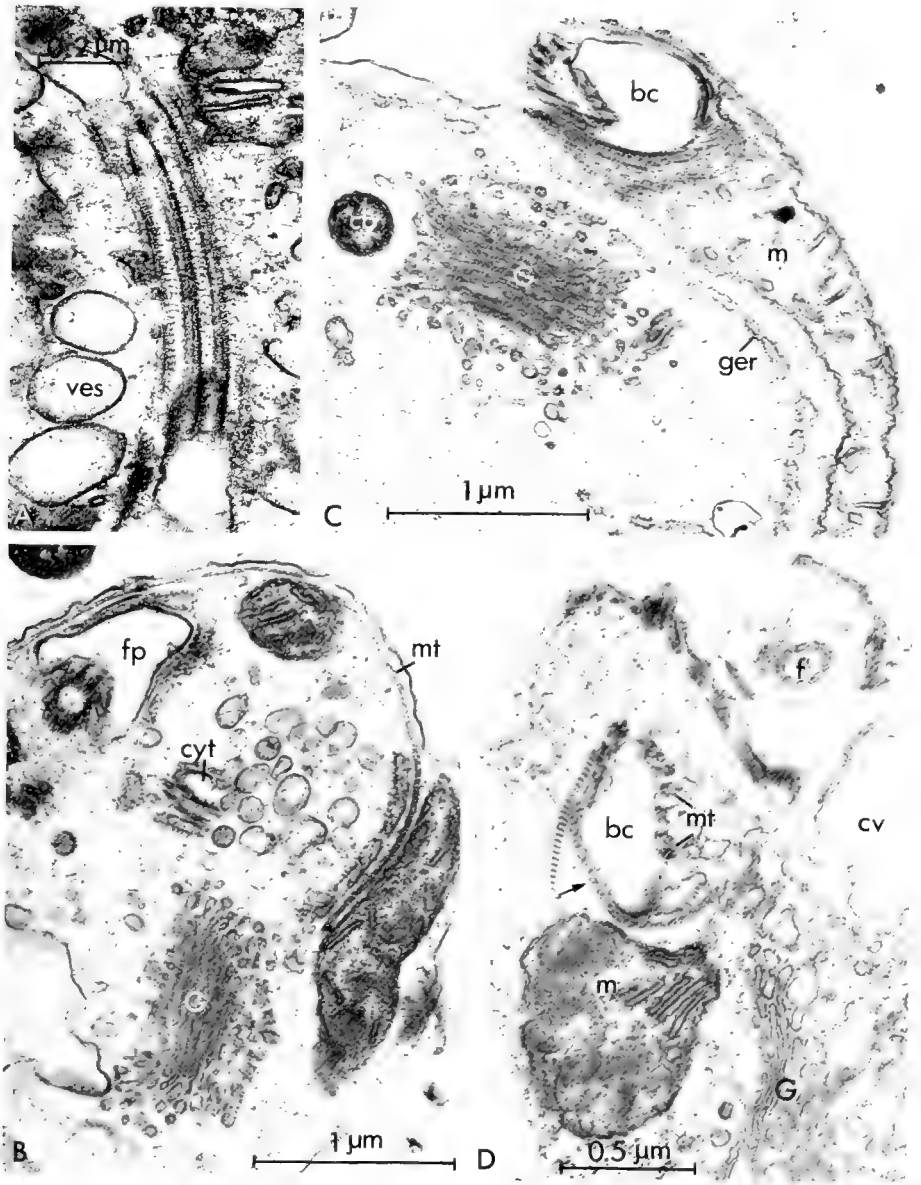

0·2 µm
ves
A
bc
m
ger
1 µm
C
fp
mt
cyt
B
1 µm
f
bc
mt
cv
m
G
0·5 µm
D

PLATE 5

FIG. A. Transverse section of the buccal cavity posterior to that shown in Pl. 4, Fig. D. The microtubules associated with the buccal cavity (between arrows) progressively move away from it. · 50,000

FIG. B. Transverse section through the beginning of the cytopharynx of *B. caudatus*. The microtubules are arranging themselves around its walls. Microtubules associated with the cytopharynx are the same set as shown in the previous figure (between arrows). · 50,000.

FIG. C Section of the mitochondrion showing the electron dense bodies which are sometimes found in the matrix · 24,000

FIG. D. Longitudinal section through *B. saltans* showing the mitochondrion passing to one side of the buccal cavity before travelling to the posterior end of the cell. Other features include the nucleus, food vacuoles and Golgi apparatus. · 15,500

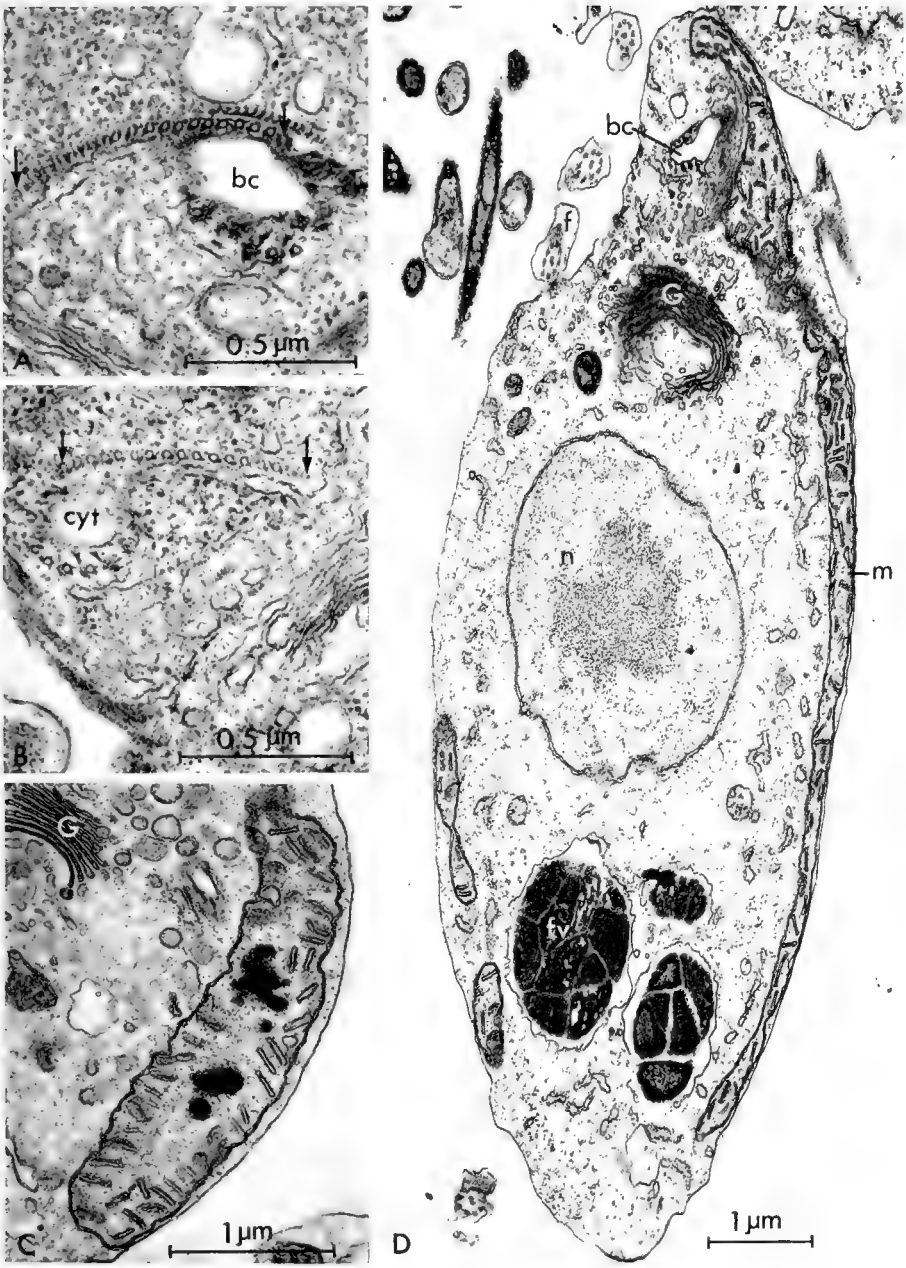
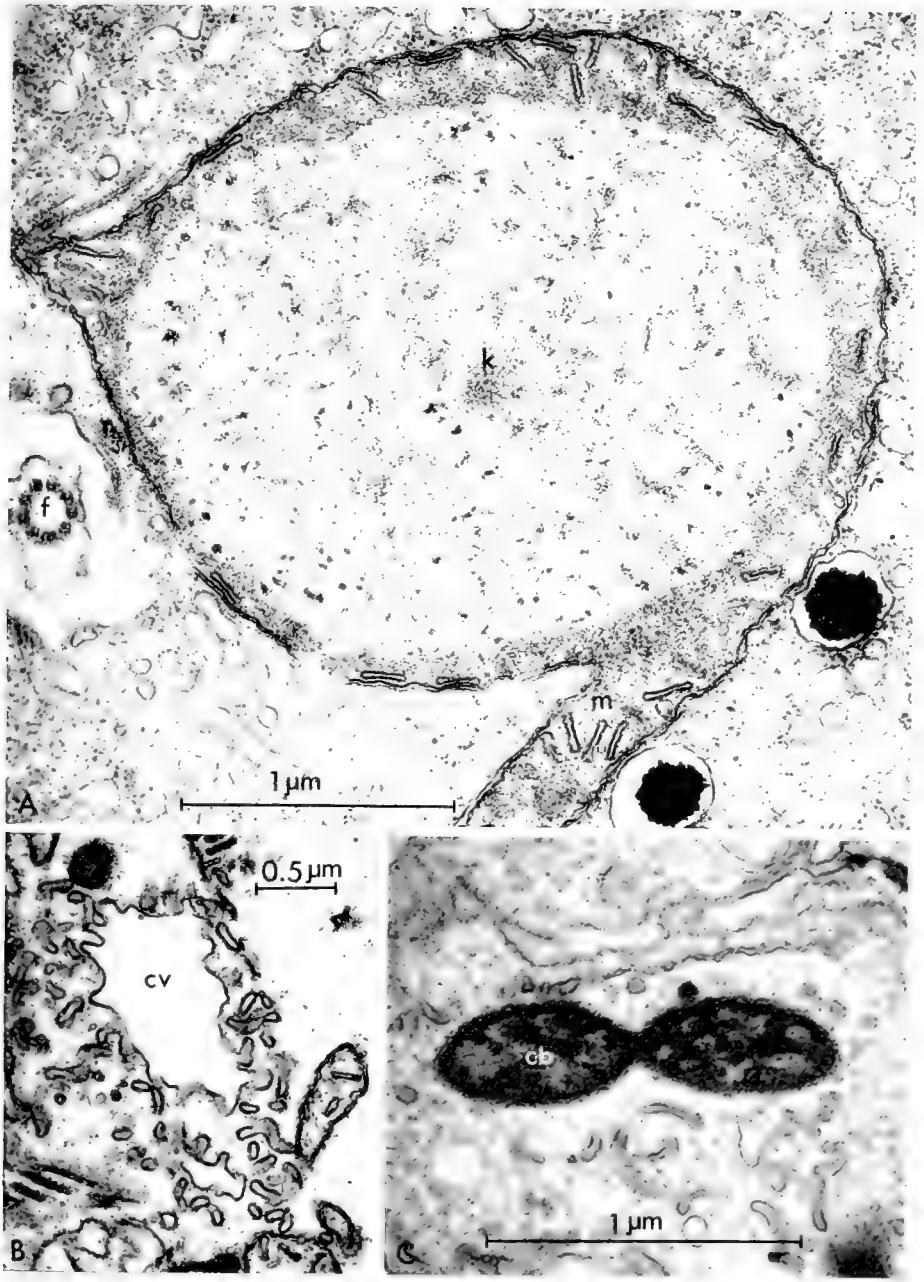

bc
0.5 µm
A
cyt
0.5 µm
B
G
1 µm
C
bc
G
n
m
fv
1 µm
D

PLATE 6

FIG. A. Section through the flat plane of the kinetoplast of *B. caudatus*. Note that the kinetoplast is composed of a reticulum of fine filaments with electron dense nodes interspersed between them. The matrix of the mitochondrion is visible at the periphery of the kinetoplast. × 40,000

FIG. B. Contractile vacuole and spongiome of *B. saltans*. × 24,000.

FIG. C. Cytoplasmic bacterium of *B. saltans* in division. × 46,000.


k
f
m
1 µm
A
0.5 µm
cv
B
cb
1 µm
C

A LIST OF SUPPLEMENTS TO THE ZOOLOGICAL SERIES OF THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY)

1. KAY, E. ALISON. Marine Molluscs in the Cuming Collection British Museum (Natural History) described by William Harper Pease. Pp. 96; 14 Plates. 1965. (Out of Print.) £3.75.
2. WHITEHEAD, P. J. P. The Clupeoid Fishes described by Lacepede, Cuvier and Valenciennes. Pp. 180; 11 Plates, 15 Text-figures. 1967. £4.
3. TAYLOR, J. D., KENNEDY, W. J. & HALL, A. The Shell Structure of Mineralogy at the Bivalvia. Introduction. Nuculacea-Trigonacea. Pp. 125; 29 Plates, 77 Text-figures. 1969. £4.50.
4. HAYNES, J. R. Cardigan Bay recent Foraminifera (Cruises of the R.V. *Antur*) 1962–1964. (*In press.*)

Printed in England by Staples Printers Limited at their Kettering, Northants, establishment

THE TYPE SPECIMENS AND IDENTITY OF THE SPECIES DESCRIBED IN THE GENUS *LITHOBIUS* BY C. L. KOCH AND L. KOCH FROM 1841 TO 1878 (CHILOPODA : LITHOBIOMORPHA)

E. H. EASON

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 22 No. 4
LONDON : 1972

THE TYPE SPECIMENS AND IDENTITY OF THE SPECIES DESCRIBED IN THE GENUS *LITHOBIUS* BY C. L. KOCH AND L. KOCH FROM 1841 TO 1878 (CHILOPODA : LITHOBIOMORPHA)

BY

EDWARD HOLT EASON

Bourton Far Hill, Moreton-in-Marsh, Gloucestershire

Pp. 103–150; 7 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 22 No. 4
LONDON : 1972

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 22, *No.* 4 *of the Zoological series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation
Bull. Br. Mus. nat. Hist. (Zool.)

© Trustees of the British Museum (Natural History), 1972

TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 3 *March*, 1972 *Price* £1.40

THE TYPE SPECIMENS AND IDENTITY OF THE SPECIES DESCRIBED IN THE GENUS *LITHOBIUS* BY C. L. KOCH AND L. KOCH FROM 1841 TO 1887 (CHILOPODA : LITHOBIOMORPHA)

By E. H. EASON

INTRODUCTION

Carl Ludwig Koch (C. L. Koch) described fifteen nominal species of *Lithobius*. His son, Dr. Ludwig Carl Christian Koch (L. Koch) redescribed most of his father's species and described thirty-two more and one variety. Subsequent authors have placed various interpretations on L. Koch's work, Latzel (1880) and Haase (1880) giving the earliest detailed and accurate accounts of what they considered to be the Kochs' western European species. These two authors, who were in correspondence with L. Koch and had access to some of his material, are in general agreement with one another and Latzel is universally recognized as the first authoritative reviser of both C. L. Koch's and L. Koch's species, although he dealt only with those found in the Austro-Hungarian Monarchy. But in spite of Latzel's and Haase's work there is still uncertainty as to the identity of some of these species whereas most of those originally described by L. Koch from Greece and from Tinos in the Aegean Archipelago have never been revised and their identity has not hitherto been established.

Carl Koch gave a very brief account of the Koch Collection of Arachnida and Myriapoda (C. Koch, 1910) but he did not mention any species by name and merely enumerated those of each class attributable to C. L. Koch and to L. Koch. I have recently been able to examine the specimens of *Lithobius* in this Collection, the bulk of which is preserved in the British Museum (Natural History) and the remainder in the Zoological Museum, Berlin. It includes the original material of two of C. L. Koch's and twenty-three of L. Koch's species together with the specimens of ten of C. L. Koch's on which L. Koch seems to have based his redescriptions. The type specimens and identity of *L. grossipes* C. L. Koch and *L. litoralis* L. Koch have been discussed in a previous publication (Eason, 1970a) and in the present paper an attempt is made to determine the identity of the other species.

SPECIES DESCRIBED BY C. L. KOCH

The original descriptions of these species (1841, 1844, 1847) are very inadequate by modern standards, relying to a large extent on details of colour and other superficial features and omitting many of the characters now recognized as of taxonomic importance. Although habitat is mentioned, type localities are indefinite. In a later publication (C. L. Koch, 1863) amplified descriptions, coloured plates and line drawings are provided but in only a few cases are they of any real value. L. Koch

(1862) was the first to redescribe these species more adequately and it is reasonable to assume that he interpreted most of his father's original descriptions correctly.

According to C. Koch (1910) only a small minority of C. L. Koch's species of Myriapoda are represented in the Koch Collection by type specimens and L. Koch did not use the original material of his father's species of *Lithobius* for many of his redescriptions. Only *L. grossipes* and *L. melanocephalus* seem to have been redescribed from type specimens, both of which are present in the Collection. Of the other species, eleven were almost certainly redescribed from specimens L. Koch either collected himself, mostly from Nuremberg and the surrounding Franconian Jura, or had sent him by other collectors: all these specimens except those of *L. impressus* are present in the Collection. The remaining species, *L. glabratus* and *L. varius*, were unknown to L. Koch.

The original material belonging to all but two of C. L. Koch's species had probably already been either lost or badly damaged before 1862. The fact that C. L. Koch's later descriptions and illustrations did not appear until 1863 is no evidence of the continued existence of these specimens; the author died in 1857 so his book must have been compiled from earlier work and suffered delay in publication. It is therefore necessary to select neotypes from L. Koch's material for six of C. L. Koch's species whose identity needs to be established in order to ensure stability of nomenclature.

SPECIES DESCRIBED BY L. KOCH

The original descriptions of most of these species (1862, 1867, 1878) are fairly adequate. The number of antennal articles, prosternal teeth, coxal pores, tergal projections, and ventral spines on the fifteenth legs are all recorded, the ocelli are figured in many cases and the female gonopods are described where females were available. A notable omission, however, is any mention of coxolateral spines (VaC) or accessory apical claws on the fifteenth legs. Fairly definite type localities are given for most of the species but type specimens are not designated.

Of the twenty-three species and one variety represented by original material in the Koch Collection, eight were based on single specimens (holotypes) and sixteen on more than one specimen (syntypes): it is necessary to select lectotypes from only seven of the latter in order to ensure stability of nomenclature. Three further species are represented in the Collection by specimens apparently identified by L. Koch but which do not seem to belong to the original material. Two of these together with a further six which are not represented were all originally described from borrowed specimens which may never have formed part of the Collection. The chief source of these specimens was the collection of Graf von Keyserling of Munich. Part of the latter, consisting largely of insects, has been acquired by the British Museum (Natural History) but all attempts to trace the specimens of *Lithobius* both here and in the principal museums of Germany and Austria have failed.

METHODS

All the species described in the genus *Lithobius* by C. L. Koch and L. Koch are recorded in order of their dates of publication whether or not there is any material available for examination. Where more than one description applying to the

same zoological species occurs in the same work, whichever name Latzel (1880), their first reviser, believed to attach to the best description is regarded as having priority even though it may appear on a later page (Code, article 24a).

All the specimens in the Koch Collection labelled with the name of a species of *Lithobius* originally described either by C L. Koch or L. Koch have been examined. They are all preserved in spirit, each tube of specimens containing labels bearing the identity, usually the locality and sometimes the habitat and name of the collector. The labels belonging to the specimens in the Zoological Museum, Berlin have all been rewritten but at least one label in each of the tubes in the British Museum (Natural History) appears to be in L. Koch's hand.

In some instances L. Koch placed specimens of different species bearing a superficial resemblance to one another under the same name. Although he made relatively few mistakes over males which usually have the most characteristic features, he had difficulty in identifying females of similar species. For example, he failed altogether to recognize females of *L. muticus* C. L. Koch, placing nearly all of them with *L. mutabilis* L. Koch and identifying as *L. muticus* females of *L. pelidnus* Haase. On the other hand he never placed widely different stadia of the same species together and regarded many of them as taxonomically distinct. In the present study each specimen is recorded under the name given it by L. Koch but those he misdetermined are also given their correct identity and placed in separate tubes, retaining their original registered numbers. All labels are recorded exactly as written by Koch. Where they have been rewritten by some recent museum worker this is indicated: where they are difficult to interpret extra words of explanation are inserted and enclosed in square brackets. Descriptions of specimens are only given when some special feature or aberration requires emphasis, or when an adequate account of the species in question is not to be found in the literature; otherwise reference is made to a published description. When it is necessary to refer to an immature post-larval stadium, Verhoeff's (1905) terms are used for the larger species such as *L. forficatus* in which the life-history is well-known, but for the smaller species to which Verhoeff's terms cannot be strictly applied, the specimen are allotted to stadia corresponding to those described for *L. variegatus* Leach (Eason, 1964).

Selected neotypes and lectotypes are labelled as such and placed in separate tubes. Selection of the former presents no difficulty but some of the syntypical series of L. Koch's species for which lectotypes are selected consist of specimens belonging to more than one zoological species; here a lectotype is selected from the specimens answering most closely to the original description of the species in question, or where there is nothing to choose between them in this respect, from those belonging to the zoological species to which it is desirable to attach Koch's name in order to cause the least confusion in current nomenclature. The originally published type localities of most of C. L. Koch's and many of L. Koch's species are vague or equivocal: in these cases the designate type locality is that of the type specimen.

Conclusions as to the status and present generic classification of all the species described by C. L. Koch and L. Koch in the genus *Lithobius* together with their published and designate type localities, are summarised in Table 1.

1. *Lithobius impressus* C. L. Koch

Lithobius impressus C. L. Koch, 1841 : 224. 1863, **1** : 115, fig. 105a, b & c. L. Koch, 1862 : 36, fig. 7a & b.

TYPE LOCALITY. Algerian coast.

MATERIAL EXAMINED. "L. impressus [rewritten]" "Corsica, [*leg.*] E. Simon" B.M.(N.H.) Reg. no. 13.6.18.326–340. Fifteen specimens which answer to the original description of *Lithobius impressus corsicus* Léger and Duboscq, 1903.

REMARKS. Since the type locality is Algeria and L. Koch's description was based on specimens from Algiers and Oran borrowed from the Kyeserling Collection, none of the above specimens from Corsica can be selected as neotype. L. Koch must have identified them after finishing his book without attaching any significance to the hooked spine (DpP) on the 14th male prefemur which is characteristic of subsp. *corsicus* (Léger & Duboscq, 1903: 316, fig. 1) but never found in the North African form.

Silvestri (1897) regarded *L. nudicornis* Gervais as the correct name for this species but most authors reject *nudicornis* which was described very scantly from a Sicilian specimen (Gervais, 1837). On the other hand *impressus* is also rejected by many authors in favour of *L. elongatus* Newport which was published some years later (Newport in Lucas, 1849). However, quite apart from the fact that *impressus* takes precedence over *elongatus* there are good reasons for supposing that these names apply to two distinct subspecies (Eason, 1971) and the valid name for the common Algerian form, which belongs to the genus *Eupolybothrus* Verhoeff and the subgenus *Allopolybothrus* Verhoeff as emended by Jeekel (1967), is *Eupolybothrus* (*Allopolybothrus*) *impressus impressus* (C. L. Koch).

2. *Lithobius dentatus* C. L. Koch

Lithobius dentatus C. L. Koch, 1844 : 22, fig. 22. 1847 : 148. 1863, **1** : 117, fig. 106a, b & c. L. Koch, 1862: 54, fig. 18.

TYPE LOCALITY. Germany.

MATERIAL EXAMINED. "Lithobius dentatus C. L. Koch, Nürnberg, leg. L. Koch [rewritten]" Zool.Mus.Berlin: Kat.Nr.333. A male and a female, both mutilated.

"Lithobius dentatus C.K." "Eichstaedt, Happurg, Nürnberg" B.M.(N.H.) Reg. no. 13.6.18.130–136. Six more or less mutilated specimens.

"Lithobius dentatus C.K." "Kärnthen [Carinthia, Austria]" B.M.[N.H.] Reg. no. 13.6.18.137. Two males and a female in fair condition.

"Lithobius dentatus C.K." "Meran [Merano, Italy], [*leg.*] Milde" B.M.(N.H.) Reg. no. 13.6.18.138. A mutilated male.

TYPE SPECIMEN. The best preserved specimen from Germany, a male 12 mm long answering to Latzel's (1880 : 81) description of *L. dentatus* var. *alpestris*, is here formally designated as the neotype (B.M.(N.H.) 13.6.18.135). Of the localities given for this specimen, Happurg is 25 km. from Nuremburg and Eichstätt (= Eich-

staedt) is only 60 km. distant, so the designate type locality may be given as "Nuremberg district".

REMARKS. Since neither C. L. Koch nor L. Koch mentioned the dorsal sulci on the 14th and 15th male tibiae, Latzel believed he had discovered a new variety characterized by these sulci which he called *alpestris*. However, the tibial sulci are quite distinct in the neotype and in the only other males in the Collection with the 14th and 15th legs intact; they were also noted by Haase (1880 : 24) as characteristic of the species so it is clear that they were merely overlooked by the Kochs and var. *alpestris* should be disregarded.

3. ***Lithobius calcaratus*** C. L. Koch

Lithobius calcaratus C. L. Koch, 1844 : 23, fig. 23. 1863, **2** : 45, fig. 168 a & b. L. Koch, 1862 : 70, fig. 30.

TYPE LOCALITY. Germany.

MATERIAL EXAMINED. "Lithobius calcaratus C. L. Koch, Franconia (Jura), leg. L. Koch [rewritten]" Zool. Mus. Berlin: Kat. Nr. 337. Four males and a female.

"Lithobius calcaratus C.K." "Nürnberg" B.M.(N.H.) Reg. no. 13.6.18.18–33. Eight males and eleven females.

"Lithobius calcaratus C.K." "fränk. Jura" B.M.(N.H.) Reg. no. 13.6.18.34–44. Seven males and a female together with three females of *L. pelidnus* Haase.

"Lithobius calcaratus C.K." "München" B.M.(N.H.) Reg. no. 13.6.18.45. A female of *L. muticus* C. L. Koch.

"Lithobius calcaratus C.K." "Rom, [*leg.*] Seidlitz" B.M.(N.H.) Reg. no. 13.6.18. 46–52. Three males and two females together with four females of *L. erythrocephalus* C. L. Koch.

"calcaratus? Nürnberg" B.M.(N.H.) Reg. no. 13.6.18.53–55 (part). A female each of *L. muticus*, *L. mutabilis* L. Koch and *L. pusillus pusillifrater* Verhoeff.

"Lithobius calcaratus C.K." "Nürnberg, missbildung der Analbeine" B.M.(N.H.) Reg. no. 13.6.18.53–55 (part). A male with the left 15th leg missing and the right 15th leg imperfectly regenerated without a femoral process.

TYPE SPECIMEN. A well-preserved male 10·5 mm long from Nuremberg answering to Latzel's (1880 : 105) description of *L. calcaratus* is here formally designated as the neotype (B M.(N.H.) 13.6.18.18).

REMARKS. All the above males, which are either fully mature or 4th post-larval stadia with the femoral process on the 15th leg at least partly developed, are correctly labelled as we would expect, since they are easily identified from C. L. Koch's original description and illustration; but of the twenty-six females L. Koch labelled "*L. calcaratus*", no fewer than eleven were misdetermined. In fact, females of this species are quite easy to identify owing to the characteristic arrangement of the ocelli and the spinulation of the legs, and Koch may have been misled by colour, a rather variable feature to which he paid undue attention in his descriptions.

In one of the males from the Franconian Jura (B.M.(N.H.) 13.6.18.41) both 15th

legs are missing but a femoral process is present on the right 14th leg. This last character was used by Matic (1961) to define *Lithobius lanzae* Matic which therefore seems to be based on an aberrant specimen of *L. calcaratus*.

4. ***Lithobius communis*** C. L. Koch

Lithobius communis C. L. Koch, 1844 : 24, fig. 24. 1863, **2** : 47, fig. 169a & b. L. Koch, 1862 : 80, fig. 37.

TYPE LOCALITY. Germany.

MATERIAL EXAMINED. "Lithobius communis C. L. Koch, Nürnberg, leg. L. Koch [rewritten]" Zool. Mus. Berlin: Kat. Nr. 341. A male and a female, both mutilated 3rd post-larval stadia of *L. mutabilis* L. Koch.

"Lithobius communis C.K." "fränk. Jura" B.M.(N.H.) Reg. no. 13.6.18.64–86. Twelve immature males of *L. mutabilis*, four being 2nd post-larval stadia and eight being 3rd post-larval stadia. In addition there are four males and three females of *L. pusillus pusillifrater*, three immature males of *L. pelidnus* and two immature males of *L. muticus*.

"Lithobius communis C.K." "[hab.] Haspelmooz" B.M.(N.H.) Reg. no. 13.6.18.87. A mutilated female 3rd post-larval stadium of *L. mutabilis* and a female 4th post-larval stadium probably belonging to *L. lapidicola* Meinert (*sensu* Jeekel, 1964 *non* Latzel, 1880).

"Lithobius communis C.K." "Cusel [Rhineland Palatinate]" B.M.(N.H.) Reg. no. 13.6.18.88. A mutilated male 3rd post-larval stadium of *L. mutabilis*.

REMARKS. Of the above specimens, only the 3rd post-larval stadia of *L. mutabilis* agree exactly with L. Koch's description of *L. communis*. All that needs to be added to this description is that the ventral spine on the 15th tibia is VaT, an accessory apical claw is present on the 15th leg, and T.13 bears feeble posterior projections. Latzel (1880 : 102) suggested that L. Koch's description was based on immature specimens of *L. mutabilis* with the possible inclusion of males of *L. muticus* and *L. pelidnus;* he added that he had actually examined two of L. Koch's specimens of "*communis*" and found them to be immature males of *L. mutabilis* and *L. pelidnus*. However, neither the specimens of *muticus* nor those of *pelidnus* labelled "*communis*" by L. Koch have either the full complement of three ventral femoral spines or the single ventral tibial spine on the 15th leg as recorded by him for this form; nor are these spines present in *L. pusillus pusillifrater* in which the antennae are much shorter than in the example of *L. communis* illustrated by C. L. Koch (1863: fig. 169a). This last illustration does, in fact, resemble *L. mutabilis* more than any other species.

Latzel's tentative suggestion that *L. communis* C. L. Koch, 1844 is a synonym of *L. mutabilis* L. Koch, 1862 is therefore almost certainly justified and has been accepted by Haase (1880) and subsequent authors. But the name *L. communis* has not actually been used except as a junior synonym since Rosicky (1876) redescribed the species, and its revival would only cause confusion. It is intended therefore to ask the International Commission on Zoological Nomenclature to use its plenary powers

to supress the name *communis* C. L. Koch 1844 as published in the binomen *Lithobius communis* C. L. Koch, and to supress the name *minutus* C. L. Koch 1847 as published in the binomen *Lithobius minutus* C. L. Koch (see p. 118), as so to validate *Lithobius mutablis* L. Koch.

5. ***Lithobius grossipes*** C. L. Koch

Lithobius grossipes C. L. Koch, 1847 : 146. 1863, **1** : 67, fig. 57a, b & c. L. Koch, 1862 : 32, fig. 4.

TYPE LOCALITY. Triest.

TYPE SPECIMEN. The holotype. B.M.(N.H.) Reg. no. 13.6.18.262.

REMARKS. All the specimens identified as *L. grossipes* by L. Koch are in the British Museum (Natural History) and were discussed in a previous publication (Eason, 1970a). Reasons for believing that a female from Idrija is the holotype were given and it was shown that *Eupolybothrus grossipes* (C. L. Koch) is a valid species and not a synonym of *E. fasciatus* (Newport) as was previously supposed.

6. ***Lithobius punctulatus*** C. L. Koch

Lithobius punctulatus C. L. Koch, 1847 : 147. 1863, **1** : 68, fig. 58a & b.? L. Koch, 1862 : 30, fig. 3.

TYPE LOCALITY. Triest.

MATERIAL EXAMINED. "L. punctulatus [rewritten]" "Dalmatien" B.M.(N.H.) Reg. no. 13.6.18.586. A mutilated female of *Eupolybothrus* sp. 25 mm long with no legs and broken antennae.

"L. punctulatus [rewritten]" "Griechenland" B.M.(N.H.) Reg. no. 13.6.18.587–588. Two cleared fragments of *Eupolybothrus* sp. with neither legs nor antennae, one from the head to T.9, the other from T.4 to the end of the body. Although obviously from different individuals, these fragments both seem to belong to the same species.

REMARKS. L. Koch's account of *L. punctulatus* was based on examples from Dalmatia and Greece with all their legs missing so there is little doubt that the above specimens are those in question. This account describes the tergal projections as short and broad which led Latzel (1880 : 56) to suspect that L. Koch was describing examples of *Eupolybothrus leptopus* (Latzel): but the shape of these projections in all three specimens is quite consistent with a diagnosis of one of the *fasciatus-grossipes* group of species. The Dalmatian specimen, however, has 11, 19, 21 and 21 coxal pores on the 12th to 15th legs respectively and this reduced number of pores, particularly those of the 12th, relative to those found in most examples of *E. grossipes* and related species of comparable size, is indeed rather suggestive of *E. leptopus*. On the other hand the fragment from Greece (with 24, 30, 32 and 27 coxal pores) is, in view of its locality, more likely to belong to *E. litoralis* (L. Koch), a species very close to *E. grossipes*.

C. L. Koch's descriptions and illustrations of *L. punctulatus* are difficult to interpret; there is no special reason to suppose that they apply either to *E. leptopus* or *E. litoralis*. Meinert (1872) used the name *L. punctulatus* C. L. Koch (probably correctly) to apply to *E. grossipes* but Latzel (1880 : 52) argued that C. L. Koch's original (1847) and subsequent (1863) descriptions of *punctulatus* do not apply to a species of *Eupolybothrus* at all but to *Lithobius validus* Meinert, 1872. Latzel's opinion has been accepted by some authors although Meinert's name for the latter species continues to be used by others. Owing to the uncertainty surrounding the identity of C. L. Koch's original specimen and of those L. Koch used for his redescription, *L. punctulatus* should be rejected as a *nomen dubium* and the species with which Latzel equated it should be known as *Lithobius validus* Meinert.

7. ***Lithobius montanus*** C. L. Koch

Lithobius montanus C. L. Koch, 1847 : 148. 1863, **2** : 8, fig. 132a & b. L. Koch, 1862 : 27, fig. 1.

Type locality. South Tyrol.

Material examined. "Lithobius grossipes C.K." "Seiseralpe [an alpine hut in Italy], [*leg.*] Gredler" B.M.(N.H.) Reg. no. 13.6.18.266. A male of *Eupolybothrus grossipes* 35 mm long, agreeing in detail with L. Koch's description of *L. montanus*.

Remarks. L. Koch's rediscription of this form was based on a single male sent him by Prof. P. Gredler from "Seiseralpe" in South Tyrol so the above specimen is undoubtedly the one in question. C. L. Koch in his original (1847) and subsequent (1863) accounts of *L. montanus* described the colour as uniform reddish-brown, and his coloured plate (1863: fig. 132a) is of a pale brown specimen without the dark dorsal pattern he illustrated in a comparable coloured plate of *L. grossipes* (1863: fig. 57a). L. Koch described the colour of *L. montanus* as paler anteriorly than posteriorly, making no mention of a dark pattern, and it seems that this relatively pale colour together with a trivial structural aberration in the holotype of *L. grossipes* mentioned in his key led him to copy his father in supposing that *montanus* and *grossipes* were distinct species. Sometime between finishing his book and completing his collection he must have decided to discard these two characters as a means of differentiating species, changing the name of his specimen from *montanus* to *grossipes*. Latzel (1880 : 48), while recognizing *L. montanus* as a synonym of *L. grossipes*, pointed out that it differs in colour from his own specimens, and Dalla Torre (1882) and Attems (1929) both retained the name *montanus* for a pale variety of *L. grossipes*. Although the holotype of *L. grossipes* has been dried and the original colour pattern had probably been lost before it was examined by L. Koch, many preserved specimens of *L. grossipes* show more evidence of a dark pattern than does L. Koch's specimen of *montanus*. However, colour is a poor taxonomic character in the Lithobiidae and there is no justification for regarding *L. montanus* as other than a synonym of *L. grossipes*.

8. ***Lithobius glabratus*** C. L. Koch

Lithobius glabratus C. L. Koch, 1847 : 149. 1863, **1** : 131, fig. 121a & b.

TYPE LOCALITY. Bavaria.

REMARKS. L. Koch (1862) was not familiar with this species and there is no material referable to *L. glabratus* in the Koch Collection. Latzel, however, was satisfied as to its identity and gave a full description (Latzel, 1880 : 74). Pocock (1890), after examining the type specimen of *L. melanops* Newport, 1845, proposed *L. glabratus* as a synonym and this species is now universally known as *L. melanops* Newport (see also Eason, 1971).

9. ***Lithobius agilis*** C. L. Koch

(Fig. 1)

Lithobius agilis C. L. Koch, 1847 : 149. 1863, **1** : 132, fig. 122a & b. L. Koch, 1862 : 52, fig. 17.

TYPE LOCALITY. Bavaria.

MATERIAL EXAMINED. "Lithobius agilis C. L. Koch, Nürnberg, leg. L. Koch [rewritten]" Zool. Mus. Berlin: Kat. Nr. 334. A male and a female, both mutilated. "Lithobius agilis C. Koch" "Mögeldorf, [hab.] Erlenwälddren" B.M.(N.H.) Reg. no. 13.6.18.4–8. Three males and two females in fair condition.

TYPE SPECIMEN. A fairly well-preserved female 9·5 mm long from Mögeldorf near Nuremburg answering to Latzel's (1880 : 78) description of *L. agilis* is here formally designated as the neotype (B.M.(N.H.) 13.6.18.4).

REMARKS. The spurs on the gonopods of the neotype (Fig. 1) and the only other female in the Collection with intact gonopods (Kat. Nr. 334) are just as slender as those figured by Loksa (1948: fig. 3) as characteristic of *L. agilis pannonicus* Loksa from Hungary, although they are rather less expanded in the distal one third with the extremity less obviously serrate. Neither L. Koch nor Latzel figured these spurs but they both described them as long and slender. Loska may have been misled into assuming that the typical form of the species bears relatively short, stout spurs by Brolemann's (1930: fig. 429) figure of a specimen of *L. agilis* from the Pyrenees in which the external spur is barely three times longer than broad. The spurs of specimens of this species from Austria (Eason, 1964: fig. 414) are intermediate in shape between those figured by Brolemann and those of the neotype, so there is little justification for naming a subspecies on the basis of this character.

10. ***Lithiobus curtipes*** C. L. Koch

Lithobius curtipes C. L. Koch, 1847 : 150. 1863, **2** : 7, fig. 131a & b. L. Koch, 1862 : 68, fig. 29.

TYPE LOCALITY. Bavaria.

MATERIAL EXAMINED. "Lithobius curtipes C. L. Koch, Nürnberg, leg. L. Koch

[rewritten]" Zool. Mus. Berlin: Kat. Nr. 339. Four males and two females together with a male of *L. aeruginosus* L. Koch.

"Lithobius curtipes C. Koch" "Nürnberg, [hab.] Haspelmooz" B.M.(N.H.) Reg. no. 13.6.18.111–121. Four males and four females together with a male and a female of *L. aeruginosus* and an immature male of *L. crassipes* L. Koch.

"curtipes, Franzensbad [Frantiskovy Lazne, Czechoslovakia]" B.M.(N.H.) Reg. no. 13.6.18.122. A single female.

"Lithobius curtipes C. Koch" "Lithauen [Lithuania]" B.M.(N.H.) Reg. no. 13.6.18. 123–126. Three males and a female.

"curtipes?, Nürnberg" B.M.(N.H.) Reg. no. 13.6.18.127–128. Two immature males.

"L. curtipes?, Böhmen [Bohemia] [rewritten]" B.M.(N.H.) Reg. no. 13.6.18.633–636. Two males and two females.

Type specimen. A well-preserved male 9 mm long from Nuremberg answering to Latzel's (1880 : 130) description of *L. curtipes* is here formally designated as the neotype (B.M.(N.H.) 13.6.18.111).

Remarks. There is no doubt at all that the above specimens, other than the three examples of *L. aeruginosus* and the single one of *L. crassipes*, belong to the species known to western European authors as *L. curtipes:* the 15th tibial projection in the neotype and the other adult males is the same as that found in British specimens (Eason, 1951: fig. 1). The inclusion by L. Koch of examples of *L. aeruginosus* among those of *L. curtipes* may be accounted for by the fact that he based his original description of *L. aeruginosus* on immature males (one of them actually belonging to *L. curtipes*) and was unaware of the true nature of this species.

In order to understand the controversy surrounding the identity of *L. curtipes* it is necessary to consider the different interpretations placed by various authors on L. Koch's description. Since C. L. Koch only examined females he did not mention the 15th tibial projection, which is only found in males, in either of his descriptions, but L. Koch described it as *"einen kurzen kegelförmigen Forsatz."* This is both imprecise and misleading, since the projection barely assumes a conical shape even when fully developed; but L. Koch also described and figured the arrangement of the ocelli (L. Koch, 1862: fig. 29) which is fairly characteristic. Stuxberg (1871:501) described the tibial projection rather more accurately as *"en tydligt utskjutande rundad process"* (a distinct projecting rounded process) as well as describing the arrangement of the ocelli.

Confusion began when Meinert, after examining the specimens on which Porat (1869) quite correctly based his records of *L. curtipes*, noted that the ocelli were not arranged exactly as figured by L. Koch and that the projection was borne on the 5th article of the 15th leg and not on the 4th as L. Koch stated, and assumed that these specimens did not belong to *L. curtipes* but represented a form of *L. crassipes* (Meinert, 1872: 341). Meinert also assumed that the projection he found on Porat's specimens was of a different shape from the conical projection described by L. Koch which he understood to refer to a more clearly differentiated process such as that found on the 15th femur of males of *L. calcaratus:* but his description of

this projection – "*dannedes kun af et fremspringende Hjørne af Leddets Bagrand— en Rende forstattes ind paa Fremragningen*" (formed only by a projecting corner of the posterior edge of the article, with a groove running onto the projection) – is the earliest really accurate account in the literature and there is no doubt that Porat's specimens did belong to *L. curtipes*. The arrangement of the ocelli in this species can be misleading as they may occur in irregular rows rather than in a rosette (Eason, 1964: 238) and the confusion over numbering the articles of the 15th legs must have been due either to an error on the part of Koch or to a misprint. Stuxberg (1876 : 25) perpetuated Meinert's mistake and attributed his own earlier (1871) description of *L. curtipes* to *L. crassipes*.

Both Latzel (1880 : 131) and Haase (1880 : 39) rectified Meinert's mistake and gave adequate accounts of *L. curtipes* under its correct name, but they both repeated Koch's rather misleading expression, "*kurzen kegelförmigen Forsatz*", in describing the tibial projection, although Latzel supplemented this by mentioning the groove on the dorsal surface. Porat (1889) described the species correctly but gave no details of the shape of the tibial projection. It was, no doubt, the failure of most of these early western European authors to give really full and accurate accounts of the projection, and the fact that the best description, Meinert's, was attributed to *L. crassipes*, that led Muralewitsch (1926) and Loksa (1947) to apply the name *L. curtipes* C. L. Koch to an eastern European species which does not occur in Bavaria and which was originally described by Sseliwanoff (1880) from the Crimea. This species, *L. pusillus* Sseliwanoff, is very similar to *L. curtipes* but the rounded tibial projection is replaced by a small cylindrical spur very much the same in structure as the femoral process found in *L. calcaratus*, a structure wrongly envisaged by Meinert as occurring in *L. curtipes*.

Sseliwanoff (1880), who wrote in Russian, as well as describing *L. pusillus*, gave a clearly recognizable account of *L. curtipes* which he named as a new species, *L. vicinus* Sseliwanoff. Loksa (1947), who cannot have been familiar with Sseliwanoff's work, gave another very adequate account of *L. curtipes* which he named as another new species, *L. baloghi* Loksa. Some modern eastern European authors have followed Loksa's nomenclature, naming *L. curtipes*, which occurs at least as far east as the Caucasus, as *L. baloghi*, and *L. pusillus* Sseliwanoff as *L. curtipes*.

Although Sseliwanoff's paper describing *L. pusillus* appeared in volume 11 of *Trudy Russkago Entomologicheskago Obshchestva*, the volume for 1878, it was not actually published until 1880 and Garbowski (1897), assuming the name to be preoccupied by *L. pusillus* Latzel, 1880, proposed the new name *sseliwanoffi* for Sseliwanoff's species; but this proposal has never been followed. *L. pusillus* Sseliwanoff seems to have been described repeatedly by various authors either as a new species or as a subspecies of *L. curtipes*. *L. ferganensis* Trotzina may prove to be its valid name (Lignau, 1914) but Trotzina's (1893) description is not altogether clear. *L. curtipes turkestanicus* Attems, the original description of which is accompanied by an illustration of the tibial projection (Attems, 1904: fig. 2), is undoubtedly identical with *L. pusillus* Sseliwanoff and the species has recently become known as *L. turkestanicus* Attems, while the true *L. curtipes* continues to be known as *L. baloghi* in eastern Europe.

A final point of nomenclatural interest is that *L. curtipes* C. L. Koch was designated by Verhoeff (1905) as the type species of the subgenus *Monotarsobius* to which *L. turkestanicus* also belongs.

11. ***Lithobius erythrocephalus*** C. L. Koch

Fig. 2

Lithobius erythrocephalus C. L. Koch, 1847 : 150. 1863, **2** : 22, fig. 145a, b & c. L. Koch, 1862 : 68, fig. 39.

TYPE LOCALITY. Bavaria.

MATERIAL EXAMINED. "Lithobius erythrocephalus C. K." "Happurg" B.M. (N.H.) Reg. no. 13.6.18.139–141. Two males and a female.

"Lithobius erythrocephalus C.K." "[hab.] Glaishammer Wälddren" B.M.(N.H.) Reg. no. 13.6.18.142–151. Nine females together with a female of *L. mutabilis*.

"Lithobius erythrocephalus C.K." "Bozen [Bolzano, Italy]" B.M.(N.H.) Reg. no. 13.6.18.152. A single female.

TYPE SPECIMEN. A well-preserved female 13 mm long from Happurg in the Franconian Jura answering to Latzel's (1880 : 110) description of *L. erythrocephalus* is here formally designated as the neotype (B.M.(N.H.) 13.6.18.139).

REMARKS. A number of subspecies of *L. erythrocephalus* have been described depending for their definition on the shape of the spurs on the female gonopods, the sculpturing of the male 15th tibiae, the shape of the short tergites, and the number of antennal articles. The genital spurs of the neotype are figured (Fig. 2) and those of the other females recorded above are of much the same shape. The 15th tibiae of the males from Happurg are oval in cross-section, without secondary sexual characters. All specimens of both sexes have feeble posterior projections on T.13 and their antennal articles vary from 29 to 31.

The neotype and other females all agree with the modern conception of the nominate subspecies, but Dobroruka (1962) stated that the males of this subspecies have flattened 15th tibiae. This feature is not shown by the males from Happurg (the designate type locality) although other males of *L. erythrocephalus* in the Collection from the Franconian Jura labelled "*mutabilis*" by L. Koch (B.M.(N.H.) Reg. no. 13.6.18. 459–460) do have markedly flattened 15th tibiae: it thus seems that this is an unstable character, not associated with any particular subspecies (see also Eason, 1970b).

12. ***Lithobius muticus*** C. L. Koch

Lithobius muticus C. L. Koch, 1847 : 151. 1863, **1** : 118, fig. 107a & b. L. Koch, 1862 : 79, fig. 36.

TYPE LOCALITY. Bavaria.

MATERIAL EXAMINED. "muticus, Nürnberg" B.M.(N.H.) Reg. no. 13.6.18 532–533. Two females of *L. calcaratus*.

"L. muticus [rewritten]" "Eichstaedt, Happurg" B.M.(N.H.) Reg. no. 13.6.18.

534–550. Six males of *L. muticus*, six females of *L. pelidnus*, and four females and one male of *L. mutabilis*,

"L. muticus [rewritten]" "[hab.] Valzner Weiher" B.M.(N.H.) Reg. no. 13.6.18 551–562. Four males of *L. muticus* and eight females of *L. pelidnus*.

"L. muticus [rewritten]" "München" B.M.(N.H.) Reg. no. 13.6.18.536–566. Two males and a female of *L. muticus* and a female of *L. mutabilis*.

TYPE SPECIMEN. A male 13 mm long from Eichstätt or Happurg, both in the Franconian Jura, is here formally designated as the neotype (B.M.(N.H.) 13.6.18. 534). This is the largest and best preserved available specimen of *L. muticus*, showing the characteristic broad head and the small setose swelling on the 14th tibia, and agreeing in all respects with Latzel's (1880 : 116) description of males of this species.

REMARKS. The characteristic swelling on the 14th tibia of the male was not mentioned either by C. L. Koch or L. Koch in their published descriptions of *L. muticus*, but L. Koch did mention it in private correspondence with Latzel (Latzel, 1880 : 119) so there is no doubt about the identity of the males on which he based his description. The same cannot, however, be said of the females.

In his key L. Koch contrasted the incurved internal pair of spurs on the gonopods of *L. mutabilis* with the straight spurs of those of *L. muticus* in order to differentiate between females of these two species; he also described the claw of the gonopod of *L. muticus* as tripartite. In fact, incurving of these spurs, although not invariable, is usually more marked in *muticus* than in *mutabilis* and the claw of *muticus* has the external denticle so reduced as to appear bipartite. It seems, therefore, that L. Koch did not have females of *L. muticus* before him when he described this species but those of *L. pelidnus* and *L. mutabilis* in which the internal spurs, particularly in *pelidnus*, are often straight and the claw always tripartite. Most of the females of *L. muticus* in the Collection were identified by L. Koch as *L. mutabilis*.

C. L. Koch's original description of this species is unsatisfactory but his illustrations of a female (C. L. Koch, 1863: fig. 107) resemble the species regarded as *L. muticus* more than any other and there is no reason to dispute its identity.

13. ***Lithobius varius*** C. L. Koch

Lithobius varius C. L. Koch, 1847 : 151. 1863, **1** : 128, fig. 118a & b.

TYPE LOCALITY. Bavaria.

REMARKS. L. Koch (1862) was not familiar with this species and there is no material referable to *L. varius* in the Koch Collection. C. L. Koch's illustrations of a female (C. L. Koch, 1863: fig. 118) are quite consistent with Latzel's (1880 : 126) suggestion that this species may be identical with *L. aeruginosus* L. Koch, but there is no certainty of this and *L. varius* should be rejected as a *nomen dubium*.

14. *Lithobius minutus* C. L. Koch

Lithobius minutus C. L. Koch, 1847 : 152. 1863, **1** : 129, fig. 119a & b. L. Koch, 1862 : 84, fig. 40.

TYPE LOCALITY. Bavaria.

MATERIAL EXAMINED. "Lithobius minutus C. L. Koch, Nürnberg, leg. L. Koch [rewritten]" Zool. Mus. Berlin: Kat. Nr. 342. Twelve badly mutilated immature specimens of *Lithobius* sp. with neither legs nor antennae, probably 1st and 2nd post-larval stadia of *L. mutabilis*.

"L. minutus [rewritten]" "fränk. Jura" B.M.(N.H.) Reg. no. 13.6.18. 387–400. Fourteen 1st post-larval stadia of *L. mutabilis* together with a 2nd post-larval stadium of another species, probably *L. pusillus pusillifrater*.

"L. minutus [rewritten]" "[hab.] Haspelmooz" B.M.(N.H.) Reg. no. 13.6.18.401. A 4th larval stadium and three badly mutilated 1st post-larval stadia, all probably belonging to *L. pusillus pusillifrater*.

"L. minutus [rewritten]" "Nürnberg" B.M.(N.H.) Reg. no. 13.6.18.402–433. Thirty-two immature specimens of *L. mutabilis* ranging from a 4th larval stadium to 2nd post-larval stadia.

REMARKS. Of the above specimens, only the 1st post-larval stadia of *L. mutabilis* agree exactly with L. Koch's description of *L. minutus*. Latzel (1880 : 228) gave *L. minutus* as a synonym of *L. mutabilis* and Haase (1880 : 32) redescribed the form in some detail, coming to the same conclusion. Although it is undoubtedly a senior synonym of *L. mutablis* (and a junior synonym of *L. communis*), the name has not been used by subsequent authors, and, in order to validate *L. mutabilis*, it is intended to ask the International Commission on Zoological Nomenclature to use its plenary powers to suppress the name *minutus* C. L. Koch 1847 as published in the binomen *Lithobius minutus* C. L. Koch, and to supress the name *communis* C. L. Koch 1844 as published in the binomen *Lithobius communis* C. L. Koch (see also p. 111).

15. *Lithobius inermis* L. Koch

Lithobius inermis L. Koch in Rosenhauer, 1856 : 415. L. Koch, 1862 : 65, fig. 26.

TYPE LOCALITY. Malaga, Spain.

REMARKS. *L. inermis* was originally described from a specimen borrowed from the Rosenhauer Collection. Dr. Egon Popp, curator of the Zoologische Staatssammlung, Munich, informs me that many of Rosenhauer's specimens were sold to the Alte Akademie, Munich, the precursor of the Staatssammlung, but that most of them were destroyed during the Second World War. Whether the type specimen of *L. inermis* was among this material is not known, but it has not been found in Munich and there is no record of Rosenhauer having deposited any of her specimens elsewhere. Koch's earlier (1856) description of this species is very scanty but his subsequent (1862) one is recognizable and Brolemann (1926 : 264) described it very fully.

16. ***Lithobius festivus*** L. Koch

Lithobius festivus L. Koch 1862 : 29, fig. 2.

TYPE LOCALITY. Garmisch, Bavaria.

MATERIAL EXAMINED. Among the specimens Koch correctly identified as *L. grossipes* the holotype and most of the specimens from South Tyrol bear an additional name, *"festivus"*, in Koch's hand. But the only specimen of this species in the Collection from Garmisch is merely labelled *"Lithobius grossipes"* "Garmisch" (see also Eason, 1970a).

TYPE SPECIMEN. *L. festivus* was originally described from a male and a female from Garmisch borrowed from the Keyserling Collection. The specimen referred to above, a male pseudomaturus 24 mm long, in spite of being labelled *"L. grossipes"* and having 49 antennal articles (Koch gave 46–47), is in agreement with Koch's description in other respects and is undoubtedly the male in question, the sole surviving syntype (B.M.(N.H.) 13.6.18.293). The female syntype must have been returned to the Keyserling Collection and has not been found.

REMARKS. C. L. Koch based *Lithobius grossipes* on an aberrant specimen and *L. montanus* (= *grossipes*) on a specimen without the dark dorsal pattern on the tergites frequently found in *grossipes* (see p. 112). *L. festivus* was based on smaller specimens with the dorsal pattern distinct but with the ocelli of the superior row round, and not oval as in large adults. It is not surprising, therefore, that L. Koch at first thought that he was dealing with three distinct species. But it is clear from his labelling of his specimens that he later realised their true identity although he may, at one stage, have regarded *festivus* as a variety of *grossipes* and only finally as a true synonym.

17. ***Lithobius transmarinus*** L. Koch

Lithobius transmarinus L. Koch, 1862 : 33, fig. 5.

TYPE LOCALITY. New Orleans, U.S.A.

REMARKS. The identity of *L. transmarinus* is discussed along with that of the next species.

18. ***Lithobius mordax*** L. Koch

Lithobius mordax L. Koch, 1862 : 34, fig. 6.

TYPE LOCALITY. New Orleans, U.S.A.

REMARKS. *L. transmarinus* and *L. mordax* seem each originally to have been described from a single specimen, a female and a male respectively, borrowed from the Keyserling Collection: neither of these has been found. There is little in the original descriptions of these two species to suggest that they are distinct from one another and some authors have regarded them as identical. Bollman (1893) believed them both to be synonyms of *L. spinipes* Say, 1821, but Brolemann (1896) disputed this synonymy and regarded them both as distinct species. Chamberlin

(1911) at one time believed *transmarinus* to be the female of *mordax* but in a later publication (Chamberlin, 1925b) he described them as separate species of *Neolithobius* Stuxberg. These descriptions of Chamberlin's seem to apply to two distinct species and their validity has not recently been disputed.

19. ***Lithobius trilineatus*** L. Koch

Lithobius trilineatus L. Koch, 1862 : 37, fig. 8.

TYPE LOCALITY. Bahia, Brazil.

MATERIAL EXAMINED. "L. trilineatus, Bahia [rewritten]" B.M.(N.H.) Reg. no. 13.6.18.651. A female of *L. forficatus* 20 mm long with the 14th and 15th legs missing.

TYPE SPECIMEN. *L. trilineatus* was originally described from a male and a female from Bahia borrowed from the Keyserling Collection. The above specimen of *L. forficatus* agrees with this description and is undoubtedly the female in question, the sole surviving syntype. The male syntype must have been returned to the Keyserling Collection and has not been found.

REMARKS. Koch distinguished this form from *L. forficatus* by means of a number of sulci he observed on the 15th legs, but these are not reliable characters in *L. forficatus*. Synonymy of *L. trilineatus* with *L. forficatus* was first proposed by Fedrizzi (1877) and has never been disputed. As Brolemann (1909) pointed out, the species must have been introduced to Brazil.

20. ***Lithobius forficatus*** var. **villosus** L. Koch

Lithobius forficatus var. *villosus* L. Koch, 1862 : 41.

TYPE LOCALITY. Bavarian Alps.

MATERIAL EXAMINED. "Lithobius forficatus L." "var. villosus, Bayer. Alpen" B.M.(N.H.) Reg. No. 13.6.18.242. A male of *L. forficatus* 22 mm long with the 15th legs missing.

"forficatus var. villosus, Alpen" B.M.(N.H.) Reg. no. 13.6.18.245–246. A male and a female of *L. forficatus*.

TYPE SPECIMEN. *L. forficatus* var. *villosus* was originally described from a single male and although the male labelled "Bayer. Alpen" has 10, 9, 9 and 7 coxal pores on the 12th and 15th legs respectively (Koch gave 9, 9, 9, 6) it agrees with this description in other respects and is undoubtedly the holotype.

REMARKS. Koch distinguished var. *villosus* from the typical form of the species by the larger number of ocelli and coxal pores, the longer 15th legs, and a number of other quite trivial characters. Although the 15th legs of the holotype are missing, those of the other two specimens of *villosus* in the Collection are barely longer than is usual in *L. forficatus*. The other characters of the holotype also fall well within normal limits for the species and *villosus* has never been regarded as a valid variety or subspecies.

21. ***Lithobius parisiensis*** L. Koch

Lithobius parisiensis L. Koch, 1862 : 42, fig. 10.

TYPE LOCALITY. Paris.

REMARKS. The original description of *L. parisiensis* was based on a single specimen borrowed from the Keyserling Collection which has not been found. It was described, like *L. trilineatus*, as having sulci on the 15th legs, but as differing from both *L. trilineatus* and *L. forficatus* in having more ocelli (39), prosternal teeth (8 + 8) and coxal pores (9, 10, 9, 7). Stuxberg (1871) suggested *L. parisiensis* as a possible synonym of *L. forficatus* but Haase (1880), who had examined Keyserling's specimen, believed it to be a distinct species. However, all the distinctive features of this form are sometimes found in large specimens of *L. forficatus* and, although there is every possibility of an introduced centipede being found in Paris, there is no known species of *Lithobius* to which the description of *parisiensis* might apply other than *forficatus* and there is little doubt that Stuxberg was correct.

22. ***Lithobius muscorum*** L. Koch

Lithobius muscorum L. Koch, 1862 : 43, fig. 11.

TYPE LOCALITY. Germany.

MATERIAL EXAMINED. "L. muscorum [rewritten]" "[hab.] Valzner Weiher" B.M.(N.H.) Reg. no. 13.6.18.434. A female pseudomaturus of *L. forficatus* 14 mm long.

TYPE SPECIMEN. The original description of *L. muscorum* was based on a single female and agrees well with the above specimen of *L. forficatus* which is undoubtedly the holotype. No locality was given in the original description, nor is there a locality label accompanying the holotype, so the presumption is that the specimen was found somewhere in Germany.

REMARKS. Of the features Koch regarded as characteristic of this form, the circular coxal pores are commonly found in immature stadia of *L. forficatus*, the rather short antennae with only 33 articles are just within normal limits for the pseudomaturus of this species and the shape of the tergal projections which Koch mentions in his key is quite unremarkable in the holotype. Synonymy of *L. muscorum* with *L. forficatus* was first proposed by Stuxberg (1871) and has never been disputed.

23. ***Lithobius hortensis*** L. Koch

Lithobius hortensis L. Koch, 1862 : 45, fig. 12.

TYPE LOCALITIES. Nuremberg; Landstuhl, Rhineland Palatinate.

MATERIAL EXAMINED. "Lithobius hortensis L. Koch, Syntypen, Nürnberg, leg. L. Koch [rewritten]" Zool. Mus. Berlin: Kat. Nr. 335. Two male pseudomaturus and a small adult female of *L. forficatus*.

"L. hortensis [rewritten]" "Nürnberg, [hab.] in Gärten" B.M.(N.H.) Reg. no. 13.6.18.303-318 (part). Five males and eleven females of *L. forficatus*, all either praematurus, pseudomaturus or small adults.

"L. hortensis [rewritten]" "Nürnberg" B.M.(N.H.) Reg. no. 13.6.18.303–318 (part). Four exuviae of *L. forficatus*. Two appear to be from adult males, one from a male pseudomaturus and the other from a female pseudomaturus.

"L. hortensis [rewritten]" "Landstuhl" B.M. (N.H.) Reg. no. 13.6.18.319–321. Two male pseudomaturus and a small adult female of *L. forficatus*.

Type specimens. The original description of *L. hortensis* was based on a number of specimens of both sexes and all the above examples of *L. forficatus*, except the exuviae, seem to belong to the syntypical series.

Remarks. Koch distinguished this form from *L. muscorum*, with which it agrees in having circular coxal pores, by the longer antennae and the shape of the tergal projections neither of which have any taxonomic significance. In fact, the coxal pores in some of the larger and more mature syntypes are oval but in no case are they oblong or split-shaped as in most large adults of *L. forficatus*.

Synonymy of *L. hortensis* with *L. forficatus* was first proposed by Meinert (1868) and has been accepted by most authors. Latzel (1880 : 61), however, suggested that adults of *L. forficatus* with circular coxal pores might be regarded as a variety (subspecies) and Verhoeff (1937) considered this form, which he called *L. forficatus* var. *hortensis*, to be predominant in the Mediterranean region. But there is no justification for retaining *hortensis* as the name of a subspecies or even a variety since the shape of the coxal pores in adults of *L. forficatus* varies continuously, showing every gradation in shape from circular, oval, oblong to slit-shaped even in specimens from the same locality.

24. ***Lithobius sordidus*** L. Koch

Lithobius sordidus L. Koch, 1862 : 47, fig. 13.

Type locality. Munich district.

Remarks. The original description of *L. sordidus* was based on a single female borrowed from the Keyserling Collection which has not been found. It seems to apply to a pseudomaturus of *L. piceus* L. Koch with only 43 antennal articles, no ventral spines on the 15th tibia and only 2 + 2 spurs on the gonopods. Latzel's (1880 : 64) proposal of *L. sordidus* as a synonym of *L. piceus* is probably justified.

25. ***Lithobius fossor*** L. Koch

Lithobius fossor L. Koch, 1862 : 48, fig. 14.

Type locality. Grütz, near Nuremberg; Ehrenbürg, Franconian Jura.

Material examined. "Lithobius fossor L.K." "Gritz [Grütz]" B.M. (N.H.) Reg. no. 13.6.18.248. A male pseudomaturus of *L. piceus* 11.5 mm long.

"Lithobius fossor L. Koch" "Ehrenbürg" B.M.(N.H.) Reg. no. 13.6.18.249. A male pseudomaturus of *L. piceus* 12·5 mm long.

TYPE SPECIMENS. Although neither of the above specimens of *L. piceus* agrees with the original description of *L. fossor* in every detail, there is little doubt that they are the two males on which this description was based and are therefore the syntypes.

REMARKS. Koch distinguished this form from *L. sordidus* by the more numerous antennal articles and the presence of two ventral spines on the 15th tibia. The syntypes have 52 and 47 antennal articles respectively (Koch gave 49) and VaT is the only ventral spine on the 15th tibia of either specimen. A second ventral spine on this article (VmT) is most unusual in *L. piceus* and it is unlikely that Koch had any specimens before him other than these two syntypes when he wrote his rather inaccurate description. Synonymy of *L. fossor* with *L. piceus* was first proposed by Latzel (1880 : 64) and has never been disputed.

26. ***Lithobius piceus*** L. Koch

Fig. 7

Lithobius piceus L. Koch, 1862 : 49, fig. 15.

TYPE LOCALITY. Garmisch, Bavaria.

MATERIAL EXAMINED. "piceus, fränk. Jura" B.M.(N.H.) Reg. no. 13.6.18.577. A female pseudomaturus.

"piceus?, Nürnberg" B.M.(N.H.) Reg. no. 13.6.18.578–579. Two female pseudomaturus.

REMARKS. *L. piceus* was originally described from a mature female borrowed from the Keyserling Collection which has not been found. None of the above specimens belong to the original material and must have been named by Koch after he had finished writing his book. Garmisch, the type locality of *L. piceus*, is only some 200 Km. from Nuremberg and the Franconian Jura and there is no reason to doubt that the specimens from these localities are identical with the form originally described, but owing to their immaturity none of them is suitable for selection as a neotype.

Koch distinguished *L. piceus* from *L. sordidus* and *L. fossor* by the more numerous antennal articles, ocelli and coxal pores, all features of maturity. Like *fossor*, *piceus* was described as having two ventral spines on the 15th tibia, presumably VmT in addition to the usual VaT: although Haase (1880) mentioned an occasional second ventral spine on this article, it was not mentioned either by Latzel (1880) or Brolemann (1930) in their descriptions of *L. piceus*. Tobias (1969) examined 80 examples of this species from the Pyrenees and found 15VmT on one side of one individual only, so that either the type specimen was unusual or, as in the case of *L. fossor*, Koch was mistaken.

Another character Koch used to distinguish between *piceus* and *sordidus* was the number of spurs on the female gonopods, 3 + 3 in the former and 2 + 2 in the latter. The female pseudomaturus of *piceus* frequently has the full complement of 3 + 3 spurs but the internal pair are very small or may be absent. The female in the

Collection from the Franconian Jura has 3 + 3 spurs but those from Nuremberg have 3 + 2 and 2 + 2, and it was probably this that led Koch to be uncertain of their identity.

Perhaps the most significant feature shown by the above examples of *L. piceus*, as well as by both of those of *L. fossor*, is the relative slenderness of the tarsi and metatarsi of the 15th legs, the distal extremity of the tibia being broader than the base of the tarsus in the ratio 3 : 2 (Fig. 7). Brolemann's figure of *L. piceus gracilitarsis* Brolemann (Brolemann, 1930 : fig. 400) shows about the same relative change in breadth between these two adjacent articles and it seems that he (Brolemann, 1898) described this subspecies from the Pyrenees on the assumption that it differed from the typical form in this respect. However, in addition to Koch's specimens, English examples and those from Italy (Eason, 1964: figs 342 & 343), the latter answering to the description of *L. piceus verhoeffi* Demange, 1958, show that same abrupt transition in the breadth of the leg at the 15th tibiotarsal articulation so it seems that this character is widespread throughout the species. Moreover, *L. piceus gracilitarsis* was recorded by Negrea (1965) from Transylvania and by Folkmanova (1951, 1954) and Folkmanova and Lang (1955, 1960) from a number of localities in Czechoslovakia and southern Poland, and although Matic and Darabantu (1968) suggested that the slender tarsi of the specimens on which some of these records were based may be features of immaturity, this is not the case in English specimens. On the other hand Brolemann (1930 : 262) described the Alpine form of *L. piceus* (which he regarded as the nominate subspecies) as having no abrupt transition in breadth between the 15th tibia and tarsus. It we assume that most records of *L. piceus* refer to this latter form, the comparative distribution of *L. piceus* and *L. p. gracilitarsis* does not suggest that we are dealing with two subspecies but that the shape of the 15th legs in *L. piceus* is variable and that subsp. *gracilitarsis* has no real status. There is also the possibility that some records of *L. piceus piceus* in the literature may refer to a closely related species, *L. peregrinus* Latzel, 1880, in which the 15th tarsi and metatarsi are relatively stout.

27. ***Lithobius coriaceus*** L. Koch

Lithobius coriaceus L. Koch, 1862 : 51, fig. 16.

Type locality. Germany.

Material examined. "Lithobius coriaceus L.K." "fränk. Jura" B.M.(N.H.) Reg. no. 13.6.18.88–91. Two agenitalis II and a male immaturus of *L. forficatus*.

"Lithobius coriaceus L.K." "Gritz [Grütz, near Nuremberg], [hab.] Garten" B.M.(N.H.) 13.6.18.92–96. Two agenitalis I, an agenitalis II and two male immaturus of *L. forficatus*.

"Lithobius coriaceus L.K." "Dietenhofen [Franconian Jura]" B.M.(N.H.) Reg. no. 13.6.18.97. An agenitalis II of *L. forficatus*.

Type specimens. The original description of *L. coriaceus* was based on a number of specimens and all the above examples of *L. forficatus* seem to belong to the syntypical series.

REMARKS. Koch had both sexes of the stadium immaturus as well as agenitalis (which he took to be males) before him when he described this form, so the above series which does not include females is incomplete. Of the key characters given by Koch, 4 + 4 prosternal teeth is exceeded in one immaturus (4 + 5) while two ventral spines are never found on the 15th tibia of the agenitalis of *L. forficatus*, so his description is not altogether accurate. Synonymy of *L. coriaceus* with *L. forficatus* was first proposed by Stuxberg (1871) and has never been disputed.

28. ***Lithobius velox*** L. Koch

Lithobius velox L. Koch, 1862 : 56, fig. 19.

TYPE LOCALITIES. Landstuhl, Rhineland Palatinate; Franconia; Vienna district.

MATERIAL EXAMINED. "L. velox [rewritten]" "Landstuhl" B.M.(N.H.) Reg. no. 13.6.18.616–617. A male and a female of *L. melanops* Newport.

"L. velox [rewritten]" "Dietenhofen [Franconian Jura]" B.M.(N.H.) Reg. no. 13.6.18.618. A male 4th post-larval stadium of *L. melanops*.

"L. velox [rewritten]" "Wien" B.M.(N.H.) Reg. no. 13.6.18.619. A mutilated female of *L. melanops*.

TYPE SPECIMENS. The original description of *L. velox* was based on a number of specimens of both sexes and all the above examples of *L. melanops* certainly belong to the syntypical series.

REMARKS. The size, the number of ocelli, and the number of coxal pores both in Koch's description and in the syntypes are all close to the lower normal range for adults and the upper range for 4th post-larval stadia of *L. melanops*. Meinert (1868) suggested *L. velox* as a possible synonym of *L. bucculentus* L. Koch, under which he was probably describing examples of *L. melanops*. Synonymy of *L. velox* with *L. glabratus* (= *melanops*) was first proposed by Latzel (1880 : 74) and has never been disputed.

29. ***Lithobius bucculentus*** L. Koch

Lithobius bucculentus L. Koch, 1826 : 57, fig. 20.

TYPE LOCALITY. Munich district.

MATERIAL EXAMINED. "bucculentus Mein.(?), Ratzes [Rasa, Italy] leg. Milde" B.M.(N.H.) Reg. no. 13.6.18.17. A single male of *L. tricuspis* Meinert.

REMARKS. Koch's original description of *L. bucculentus* as having sharp posterior projections on T.9, 11 and 13, and the antennae and 15th legs both over half the body-length is much more suggestive of *L. tricuspis* than of *L. melanops* (of which it has hitherto been regarded as a synonym), but this description was based on a male from Munich borrowed from the Keyserling Collection which has not been found, and the specimen from Rasa in the South Tyrol is not the holotype; nor can the latter be selected as neotype as it was taken too far from the type locality and Koch was uncertain of its identity. This uncertainty may have been due to the presence, on the specimen from Rasa, of a ventral spine (VaT) on the 15th tibia, a spine which

may be absent in *L. tricuspis* (Eason, 1965) and which Koch did not mention in the original description. Although 15 VaT rarely if ever occurs in *L. melanops*, Meinert (1868) did mention a single variable ventral spine of the 15th tibia in his redescription of *L. bucculentus*, possibly because he based it on examples of *tricuspis* as well as of *melanops*, and this may have led Koch to attach Meinert's name to the specimen from Rasa which he probably examined after he had read Meinert's paper.

Stuxberg's (1871) description of *L. bucculentus* is general enough to include all species of *Lithobius* with more than seven ocelli on each side, 2 + 2 prosternal teeth, and posterior projections on T.9, 11 and 13: he included all the nominal species known to him which are embraced by this definition in his synonymy. Meinert's (1868) and Haase's (1880) descriptions of this species are identical with each other, much more restricted than Stuxberg's, and more likely to refer almost exclusively to *L. melanops*. Latzel (1880: 74) gave a full description of *L. glabratus* (= *melanops*) and proposed *L. bucculentus* as a synonym. But it is fairly certain that all these authors were mistaken and that *L. bucculentus* is the senior synonym of *L. tricuspis* Meinert, 1872. However, the name has not been used for well over fifty years and to revive it would cause confusion. It is intended therefore to ask the International Commission on Zoological Nomenclature to use its plenary powers to suppress the name *bucculentus* L. Koch 1862 as published in the binomen *Lithobius bucculentus* L. Koch, so as to validate *Lithobius tricuspis* Meinert.

30. ***Lithobius melanocephalus*** C. L. Koch

Lithobius melanocephalus C. L. Koch in L. Koch, 1862 : 58, fig. 21. C. L. Koch, 1863, **1** : 130, fig. 120a & b.

Type locality. Ehrenbürg, Franconian Jura.

Material examined. "L. melanocephalus [rewritten]" "Ehrenbürg" B.M. (N.H.) Reg. no. 13.6.18.384–385. A male and female of *L. melanops*.

Type specimens. The original description of *L. melanocephalus* was based on a male and a female and the above two examples of *L. melanops* are undoubtedly the syntypes.

Remarks. L. Koch attributed this species to his father and the later description (C. L. Koch, 1863) was no doubt made from one of C. L. Koch's specimens: but the first description to be published, based on L. Koch's two specimens, must stand as the original. There is no reason to suppose that C. L. Koch's illustration of *L. melanocephalus* refers to *L. dentatus* as Latzel (1880 : 76) suggested; in this figure (C. L. Koch, 1863: fig. 120a) the tergal projections do indeed resemble those of *L. dentatus* but the antennae are only two-fifths of the body-length with 34 articles which is typical of *L. melanops* and quite unlike *L. dentatus* in which the antennae are about three-fifths of body-length with 50 to 60 articles: C. L. Koch is likely enough to have made a slight error in outlining the shape of the tergites but is much less likely to have been mistaken over the antennae.

The size, the number of ocelli, and the number of coxal pores both in L. Koch's description and in the syntypes are close to the upper normal range for adults of

L. melanops. L. Koch described *L. melanocephalus* as resembling L. *bucculentus* (= *tricuspis*) in having three ventral spines on the 15th femur but differing in having blunt tergal projections; although a third ventral femoral spine (15VpF), which is almost invariable in *L. tricuspis*, is quite common in large specimens of *L. melanops*, it is only present on the left 15th leg of the female syntype (the 15th legs of the male syntype are missing); the tergal projections in the syntypes as in all specimens of *L. melanops* are, of course, noticeably blunter than in *L. tricuspis*.

Meinert (1872) and Haase (1880) suggested *L. melanocephalus* as a possible synonym of *L. bucculentus* under which they were probably describing examples of *L. melanops*. Latzel (1880 : 74), in spite of his doubt about the identity of C. L. Koch's figure had no doubt about L. Koch's description and was the first to propose *L. melanocephalus* as a synonym of *L. glabratus* (= *melanops*).

31. ***Lithobius venator*** L. Koch

Lithobius venator L. Koch, 1862 : 59, fig. 22.

TYPE LOCALITY. Ehrenbürg, Franconian Jura.

MATERIAL EXAMINED. "L. venator [rewritten]" "Ehrenbürg" B.M.(N.H.) Reg. no. 13.6.18.620. A female of *L. melanops* 13 mm long.

"L. venator [rewritten]" "Nürnberg" B.M.(N.H.) Reg. no. 13.6.18.621–629. Ten more or less mutilated specimens of *L. nigrifrons* Latzel and Haase.

"L. venator [rewritten]" "[?]" B.M.(N.H.) Reg. no. 13.6.18.630–631. A male and a female of *L. melanops*.

"nigrifrons? venator?, Nürnberg" B.M.(N.H.) Reg. no. 13.6.18.570–573. Four mutilated 1st post-larval stadia of *L. melanops*.

TYPE SPECIMEN. The original description of *L. venator* was based on a single female and although the above female of *L. melanops* from Ehrenbürg has 36 antennal articles (Koch gave 38) and 1 + 4, 4, 2 ocelli (Koch gave 1 +4, 4, 3 and figured 1 + 4, 3, 2) it agrees with this description in other respects and is undoubtedly the holotype.

REMARKS. Koch distinguished this form from *L. melanocephalus* by the fewer ocelli and the absence of the third ventral spine on the 15th femur, and from *L. velox* by the shape of the internal margins of the tergal projections; none of these characters has any taxonomic significance. Koch's labelling of examples of *L. nigrifrons* as *L. venator* is not surprising as this species answers equally well to the original description of *L. venator* and Latzel (1880 : 73) suspected that *nigrifrons* and *venator* might be identical. But Koch, in private correspondence with Latzel (Latzel, 1880 : 73), confirmed that his three specimens of *L. venator* (no doubt the holotype and the two specimens from an indecipherable locality) had accessory apical claws on the 15th legs, claws which are present in *L. melanops* but not in *L. nigrifrons*.

The identity of *L. venator* has not hitherto been definitely established. Meinert (1868) suggested it as a possible synonym of L. *bucculentus* (i.e. *L. melanops*). Stuxberg (1871) gave the same synonymy but also included such diverse species as

L. dentatus, *L. agilis* and *L. intrepidus* Meinert as synonyms so one cannot be sure which species he had in mind. Latzel (1880 : 74) suggested *L. venator* as a possible synonym of *L. glabratus* (= *melanops*) but he was not altogether satisfied as to its identity. The only descriptions of species under *L. venator* L. Koch, other than the original, are those of Porat (1869) and Sseliwanoff (1880); these are both difficult to interpret but they probably refer to *L. melanops*. Attems (1927) regarded *venator* as a subspecies of *L. melanops* without the accessory apical claw on the 15th leg, but this use of the name is quite wrong. *L. venator* is definitely a synonym of *L. melanops*.

32. ***Lithobius minimus*** L. Koch

Lithobius minimus L. Koch, 1862 : 61, fig. 23.

Type locality. Germany.

Material examined. "L. minimus [rewritten]" "Mögeldorf [near Nuremberg], [hab.] Erlenwälddren" B.M.(N.H.) Reg. no. 13.6.18.386. A female 3rd post-larval stadium 6·4 mm long with both 15th legs missing. This specimen belongs to one of the *lapidicola-borealis* group of species characterized by rather feeble posterior projections on T.11 and 13 only; it may very tentatively be referred to *L. salicis* Verhoeff, but the absence of the 15th legs and the immaturity of the specimen make definite identification impossible.

Remarks. The original description of *L. minimus* disagrees altogether with the above specimen which has 35 antennal articles (Koch gave 22), 1 + 4, 3, 1 ocelli (Koch gave 1 + 2, 1), 2, 2, 2, 2 coxal pores (Koch gave 1, 1, 1, 1), and 0, 1, 3, 2, 1 ventral spines on the 14th leg (Koch gave 0, 0, 1, 1, 0 on the 15th). The extent of this disagreement can hardly be accounted for by a careless description and the specimen must have been labelled in error by Koch himself or during some rearrangement of his Collection.

Latzel did not deal with this species but Meinert (1872) suggested *L. minimus* as a possible synonym of *L. bucculentus* (i.e. *L. melanops*). Koch's description, however, agrees better with the 1st post-larval stadium of *L. agilis*. But there can be no certainty about the identity of *L. minimus* and it should be rejected as a *nomen dubium*.

33. ***Lithobius immutabilis*** L. Koch

Lithobius immutabilis L. Koch, 1862 : 62, fig. 24.

Type locality. Germany.

Material examined. "Lithobius immutabilis L. Koch, Syntypen, Nürnberg, leg. L. Koch [rewritten]" Zool. Mus. Berlin: Kat. Nr. 331. Two mutilated 1st post-larval stadia of *L. dentatus*.

"L. immutabilis [rewritten]" "Mögeldorf [near Nuremberg], [hab.] Erlengebüsch" B.M.(N.H.) Reg. no. 13.6.18.322–325. A 4th larval stadium and four 1st post-larval stadia of *L. dentatus*, all more or less mutilated.

TYPE SPECIMENS. The original description of *L. immutabilis* was based on a number of specimens and all the above examples of *L. dentatus* seem to belong to the syntypical series.

REMARKS. Koch's description is clearly of a series of immature specimens and applies equally well to a number of species. Meinert (1872) and Latzel (1880 : 74) suggested *L. immutabilis* as a possible synonym of *L. bucculentus* (i.e *L. melanops*) and *L. glabratus* (= *melanops*) respectively. Only Haase (1880), who may well have seen the original material, suggested its true synonymy with *L. dentatus*.

34. ***Lithobius macilentus*** L. Koch

Lithobius macilentus L. Koch, 1862 : 63, fig. 25.

TYPE LOCALITIES. Nuremberg; Franconian Jura; Bolzano, Italy.

MATERIAL EXAMINED. "Lithobius macilentus L. Koch, Syntypen?, Nürnberg, leg. L. Koch [rewritten]" Zool. Mus. Berlin: Kat. Nr. 332. A female of *L. erythrocephalus* and two very mutilated specimens, a male and a female, probably 4th post-larval stadia of *L. mutabilis*.

"L. macilentus [rewritten]" "[hab.] Valzner Weiher, Gritz [Grütz, near Nüremberg]" B.M.(N.H.) Reg. no. 13.6.18.380–382. Two female 3rd post-larval stadia of *L. aulacopus* Latzel with 37 and 35 antennal articles respectively, together with one 1st post-larval stadium of *L. tricuspis* with 26 antennal articles, all three more or less mutilated.

"L. macilentus [rewritten]" "macilentus, Botzen [Bolzano]" B.M.(N.H.) Reg. no. 13.6.18.383 (part). A mutilated 1st post-larval stadium of *L. tricuspis* with antennae missing.

"L. macilentus [rewritten]""Happurg [Franconian Jura]" B.M.(N.H.) Reg. no. 13.6.18.383 (part). A badly mutilated fragment barely recognizable as belonging to a species of *Lithobius*.

TYPE SPECIMENS. The original description of *L. macilentus* was obviously based on two different species and there is no doubt that the above specimens from Grütz and Bolzano, and possibly also the fragment from Happurg, belong to the syntypical series. The same cannot be said of those in the Berlin Museum which bear no resemblance to Koch's description and must have been labelled by mistake. That part of Koch's description applying to the larger specimens with more than 32 antennal articles (females) together with his figure of the ocelli clearly refers to an immature example of *L. aulacopus;* the least defective of these, a 3rd post-larval stadium 8mm long with 37 antennal articles, answering exactly to Koch's description of the larger form and also to Latzel's (1880 : 85) description of the "juvenis" of *L. aulacopus*, is here formally designated as the lectotype (B.M.(N.H.) 13.6.18.380).

REMARKS. Meinert (1872) suggested *L. macilentus* as a possible synonym of *L. agilis*. Fedrizzi (1877) gave a rather diffuse account of the species which is more than mere repetition of Koch's description and, although probably composite, seems to include *L. aulacopus*. Latzel (1880 : 80) recognised the inclusion of immature examples of two separate species by Koch in his original description of *L. macilentus*

and, probably following Meinert, proposed *L. agilis* as the senior synonym to apply only to the smaller specimens with fewer than 32 antennal articles which Koch regarded as males; he made no suggestion as to the identity of the larger females with more than 32 antennal articles and dismissed Koch's description and figure of the ocelli as unreliable, going on to describe *L. aulacopus* as a new species (Latzel, 1880 : 84).

Meinert's and Latzel's failure to guess the identity of the smaller specimens is quite understandable but both of them overlooking Koch's very adequate description of the larger females is surprising. Haase (1880) followed Latzel's synonymy and all subsequent authors have accepted *L. macilentus* as a synonym of *L. agilis*.

Lohmander (1957 and *in litt.*) pointed out that *L. aulacopus* is a junior synonym of *L. intrepidus* Meinert, 1868. Most authors, however, continue to use the name *aulacopus* and the nomenclature of this species is unsatisfactory: it should now be known as *L. macilentus* L. Koch.

35. ***Lithobius alpinus*** L. Koch

Fig. 3

Lithobius alpinus L. Koch, 1862 : 66, fig. 27.

Type locality. Seiseralpe, an alpine hut in the Italian Tyrol.

Material examined. "Lithobius alpinus in Seiseralpe leg. Gredler" B.M.(N.H.) Reg. no. 13.6.18.12. A female of *L. lucifugus* L. Koch 15 mm long with oval coxal pores and most of the legs missing.

Type specimen. The original description of *L. alpinus* was based on a single defective female and agrees exactly with the above specimen of *L. lucifugus* which is undoubtedly the holotype.

Remarks. Koch used the shape of the coxal pores as a key character, separating those forms such as *L. alpinus* with oval coxal pores from species in which the pores are circular. Latzel (1880 : 122) realised that these pores may be either circular or oval in *L. lucifugus* and suggested *L. alpinus* as a possible synonym of this species. Borek (1967) argued that *L. alpinus* must be a species distinct from *L. lucifugus* owing to its small number of antennal articles (30), but this argument is not justified; the number of antennal articles is very variable in *L. lucifugus* as Borek himself pointed out.

The holotype shows a pair of small paramedian prosternal teeth not noted by Koch, in addition to the usual 2 + 2 (Fig. 3). These extra teeth are characteristic of *L. lucifugus* var. *latzeli* Verhoeff, 1935 which Verhoeff (1937) later raised to a subspecies; but the form and number of prosternal teeth in *lucifugus* are very variable, even in examples from the same locality, and there is no justification for regarding *latzeli* as a subspecies. Should it be thought necessary to give varietal status to specimens with these extra prosternal teeth, the name *latzeli* Verhoeff should be used, since the name *alpinus* must be rejected as a junior homonym of *Lithobius alpinus* Heer, 1845, which refers to an immature specimen of uncertain identity from the Swiss Alps.

36. ***Lithobius granulatus*** L. Koch

Lithobius granulatus L. Koch, 1862 : 67, fig. 28.

TYPE LOCALITY. Unknown.

MATERIAL EXAMINED. "Lithobius granulatus L.K." "Patria?" B.M.(N.H.) Reg. no. 13.6.18.258. A male of *L. lucifugus* 19 mm long with oval coxal pores and with both antennae and all the legs missing.

TYPE SPECIMEN. The original description of *L. granulatus* was based on a single male with antennae and legs missing and agrees exactly with the above specimen of *L. lucifugus* which is undoubtedly the holotype.

REMARKS. As in the case of *L. alpinus* the oval coxal pores of *L. granulatus* were used by Koch as a key character. The only trace of an appendage borne by the holotype consists of the first and second articles of the right antenna, the second of which appears unusually elongate, and it was this slight aberration which led Koch to regard *L. granulatus* as a species distinct from *L. alpinus*. There is no previously proposed synonymy for this form and very little mention of it in the literature. Sseliwanoff's (1880) description of *L. granulatus* L. Koch refers to some species other than *L. lucifugus*. *L. granulatus* Meinert, 1872 is a homonym referring to a South American species.

37. ***Lithobius crassipes*** L. Koch

Lithobius crassipes. L. Koch, 1862 : 71, fig. 31.

TYPE LOCALITY. Nuremberg district.

MATERIAL EXAMINED. "Lithobius crassipes L. Koch, Syntypen?, Franconia (Jura), leg. L. Koch [rewritten]" Zool. Mus. Berlin: Kat. Nr. 340. A male and two females.

"No. 272 Lithobius crassipes L.K. Types [rewritten]" "fränk. Jura" B.M.(N.H.) Reg. no. 13.6.18.98–110. Four males and nine females ranging in the degree of their maturity from 3rd post-larval stadia to adults.

"crassipes, Nürnberg" B.M.(N.H.) Reg. no. 13.6.18.259–261. A male and a female together with a female of *L. curtipes*.

TYPE SPECIMENS. The original description of *L. crassipes* was based on a number of specimens of both sexes. All the above specimens from the Franconian Jura, much of which lies in the Nuremberg district, seem to belong to the syntypical series, but those labelled "Nürnberg" were probably added to the Collection after the description had been written. A well-preserved adult female 8·5 mm long answering to Latzel's (1880 : 128) description of *L. crassipes* is here formally designated as the lectotype (B.M.(N.H.) 13.6.18.98).

REMARKS. The single female of *L. curtipes* from Nuremberg does not show the characteristic arrangement of the ocelli very clearly, so it is not surprising that Koch should have included it among his specimens of *L. crassipes*.

38. *Lithobius sulcatus* L. Koch

Fig. 4

Lithobius sulcatus L. Koch, 1862 : 73, fig. 32.

TYPE LOCALITY. Nuremberg.

MATERIAL EXAMINED. "L. sulcatus [rewritten]" "Happurg [Franconian Jura]" B.M.(N.H.) Reg. no. 13.6.18.599–600. A male 2nd post-larval stadium of *L. agilis* and another immature male, probably a 2nd post larval stadium of *L. crassipes*.

"L. sulcatus [rewritten]" "Gritz [Grütz], [hab.] Wälddren bin. Glaishammer" B.M.(N.H.) Reg. no. 13.6.18.601–607. Three specimens answering to Koch's description of *L. sulcatus* together with a female 3rd post-larval stadium of *L. aeruginosus* and three other immature specimens, probably a 1st post-larval stadium and female 2nd post-larval stadium of *L. curtipes* and a 1st post-larval stadium of *L. crassipes*.

TYPE SPECIMENS. The original description of *L. sulcatus* was based on a number of immature specimens and all those from Grütz, near Nuremberg, some of which bear only a superficial resemblance to one another, seem to belong to the syntypical series. One of those answering to Koch's description is here formally designated as the lectotype (B.M.(N.H.) 13.6.18.601).

REMARKS. Koch can have examined only three specimens at all carefully when writing his description of *L. sulcatus;* most of the others labelled "*L. sulcatus*" agree with this description in a few characters only and the example of *L. agilis* not at all. Latzel did not deal with the species, there is little reference to it in the literature, and it has never been redescribed although Attems (1909) referred it to the subgenus *Monotarsobius*. The following description is based on the lectotype and the other two specimens from Grütz with which it is conspecific.

DESCRIPTION. *Length:* 4·6 to 4·8 mm. *Antennae:* 1·4 to 1·5 mm long; of 21 or 22 articles. *Ocelli*: 3 or 4; a relatively small posterior ocellus, a rather larger intermediate one and one or two much smaller anterior ocelli (Fig. 4). *Prosternum:* with 2 + 2 teeth and a pair of well-developed lateral spines. *Tergites:* slightly wrinkled; general shape as in species of *Monotarsobius* with posterior angles of T.9, 11 and 13 obtusely rounded. *Coxal pores:* 1, 1, 1, 1. *Legs:* tarsus and metatarsus fused on 1st to 11th; the 14th and 15th moderately thickened; 15th accessory apical claw present. *Genitalia:* undeveloped.

Spinulation:

	Ventral					Dorsal				
	C	t	P	F	T	C	t	P	F	T
1	—	—	—	—	m	—	—	—	—	(a)
2	—	—	—	—	m	—	—	—	—	(a)
3	—	—	—	—	m	—	—	—	p	(a)
4	—	—	—	—	m	—	—	—	p	(a)
5	—	—	—	m	m	—	—	—	a–p	a–p
6	—	—	—	m	m	—	—	—	a–p	a–p
7	—	—	—	m	m	—	—	—	a–p	a–p

Spinulation:

	Ventral					Dorsal				
	C	t	P	F	T	C	t	P	F	T
8	—	—	—	m	m	—	—	—	a–p	a–p
9	—	—	—	m	m	—	—	—	a–p	a–p
10	—	—	—	m	m	—	—	(p)	p	—
11	—	—	—	m	m	—	—	p	(p)	—
12	—	—	m	m	m	—	—	(mp)	(p)	—
13	—	—	m	m	—	—	—	-	-	—
14	—	—	m	m	—	—	—	—	—	—
15	—	—	m	m	—	—	—	—	—	—

The letters enclosed in brackets indicate variable spines.

IDENTITY. These specimens are 1st post-larval stadia of a species of *Monotarsobius* which, in its adult form, would certainly have antennal articles considerably in excess of twenty. They would therefore answer to *L. microps* Meinert, 1868 (= *L. duboscqui* Brolemann), one of the few species of *Monotarsobius* with more than twenty antennal articles and a 15th accessory apical claw, were it not for the presence of such spines as DaF and DpF which are rarely found even in adults of *L. microps* (see also Jeekel, 1964). Verhoeff (1931, 1934, 1937) attached the name *microps* to one or more European species of *Monotarsobius* which differ from the true *microps* in having a more profuse spinulation. In using the name in this way Verhoeff was following Meinert who, in his redescription of *L. microps* (Meinert, 1872), included at least one other species in addition to the true *microps*. But in spite of "*L. microps*" figuring in numerous keys and brief descriptions it seems never to have been properly described except by Brolemann (1930), and there is some doubt as to whether Brolemann was describing the same species as Verhoeff. On the other hand a bewildering number of subspecies of "*microps*" have been described by Verhoeff and other authors from various parts of Europe, some in considerable detail. Although the specimens of *L. sulcatus* may possibly be examples of *L. microps* with unusual spinulation, they are more likely to be identical with the misnamed "*L. microps*" of Verhoeff or one of its subspecies. But a full description of the species must await discovery of adults in the neighbourhood of Nuremberg.

39. ***Lithobius aeruginosus*** L. Koch

Lithobius aeruginosus L. Koch, 1862 : 74, fig. 33.

TYPE LOCALITY. Nuremberg district.

MATERIAL EXAMINED. "Lithobius aeroginosus L.K." "fränk. Jura" B.M.(N.H.) Reg. no. 13.6.18.1. A male 4th post-larval stadium 5·8 mm long.

"Lithobius aeruginosus L.K." B.M.(N.H.) Reg. no. 13.6.18.2. A male 4th post-larval stadium of *L. curtipes* 7 mm long.

TYPE SPECIMENS. The original description of *L. aeruginosus* was based on at least two males and the above two specimens seem to be the syntypes. The one labelled "fränk. Jura" answers more closely to this description and also agrees with Latzel's (1880 : 126) description of *L. aeruginosus*; it is here formally designated as the lectotype (B.M.(N.H.) 13.6.18.1).

Remarks. Although both the above specimens have three ventral spines on the 15th prefemur (Koch gave one) they answer fairly well to Koch's description in other respects. The male of *L. curtipes*, however, has the characteristic tibial projection feebly but quite distinctly developed on the 15th leg, a second ventral spine (VaF) on the 15th femur, and the ocelli, though not arranged as in adults of *L. curtipes*, are in a somewhat irregular line and not in a precisely straight line as in the lectotype: Koch evidently overlooked all these details and seems to have depended more on the lectotype for his description.

The 15th legs of the lectotype are unusually long for this species (two-fifths of the body-length), a feature noted by Koch and attributed by Latzel (1880 : 128) to immaturity. But Koch regarded it as characteristic of the species and this may have led him to identify the other examples of *L. aeruginosus* in the Collection, all of which have relatively short legs, as *L. curtipes* or *L. sulcatus*.

40. ***Lithobius mutabilis*** L. Koch

Lithobius variegatus: C. L. Koch, 1844 : 21, fig. 21. 1863, **2** : 21. fig. 144a & b (*non* Leach 1814)
Lithobius mutabilis L. Koch, 1862 : 75, fig. 34.

Type locality. Germany.

Material examined. "Lithobius mutabilis L. Koch, Syntypen?, Nürnberg, leg. L. Koch [rewritten]" Zool. Mus. Berlin: Kat. Nr. 329. Four males and four females together with a female of *L. muticus*, all more or less mutilated.

"L. mutabilis [rewritten]" "fränk. Jura" B.M.(N.H.) Reg. no. 13.6.18.435–458. Five males and nine females together with five males and three females of *L. pelidnus* and a male and female of *L. muticus*.

"mutabilis, fränk. Jura" B.M.(N.H.) Reg. no. 13.6.18.459–460. Two males of *L. erythrocephalus*.

"mutabilis, Nürnberg" B.M.(N.H.) Reg. no. 13.6.18.461–520 (part). Twenty-four males (including 3rd and 4th post-larval stadia) and twenty-three females together with seven males and five females of *L. pelidnus* and an adult male, a male 3rd post-larval stadium and eight females of *L. muticus*.

"L. mutabilis [rewritten]" "Nürnberg—Einlegend ♀ mit Ei" B.M.(M.H.) Reg. no. 13.6.18.461–520 (part). A single female.

"L. mutabilis [rewritten]" "München" B.M.(N.H.) Reg. no. 13.6.18.521–526. A female 4th post-larval stadium of *L. mutabilis*, a male and a female of *L. muticus*, two females of *L. lapidicola* Meinert (*sensu* Jeekel, 1964 *non* Latzel, 1880), and two rather defective females, probably belonging to *L. subtilis* Latzel.

"mutabilis, Tirol" B.M.(N.H.) Reg. no. 13.6.18.527. A single male.

"L. mutabilis [rewritten]" "Böhmen [Bohemia]" B.M.(N.H.) Reg. no. 13.6.18. 528–531. Two males and two females.

"mutabilis, Franzensbad [Frantiskovy Lazne, Czechoslovakia]" B.M.(N.H.) Reg. no. 13.6.18.632. A single male.

Type specimens. The original description of *L. mutabilis* was based on two distinct species, *L. mutabilis* as described by Latzel (1880 : 97) and *L. pelidnus*

Haase, 1880. The specimens in the Berlin Museum and those in the British Museum (N.H.) from the Franconian Jura (13.18.6.435–458) all seem to belong to the syntypical series and a well-preserved male 10 mm long agreeing with Latzel's description of *L. mutabilis* is here formally designated as the lectotype (B.M.(N.H.) 13.6.18.435).

Remarks. L. Koch intended his description of *L. mutabilis* to apply to *L. variegatus* Leach as described by C. L. Koch in 1844 and he renamed it because he realised that Leach's (1814) description referred to an altogether different species. Although one cannot say whether C. L. Koch had before him examples of the species now recognized as *L. mutabilis*, those of *L. pelidnus*, or a mixture of the two when he wrote his description of *L. variegatus*, and his illustration of the latter (C. L. Koch, 1863: fig. 144) could apply to either species, the obvious course is to select a specimen of the former as lectotype in order to preserve current nomenclature.

Females of *L. mutabilis* and *L. pelidnus* are very difficult to distinguish from one another and it has already been shown how L. Koch came to confuse them with those of *L. muticus* (see p. 117), so most of his misdeterminations are easily explained: but the two males of *L. erythrocephalus* from the Franconian Jura and the two unexpected species from Munich bear only a superficial resemblance to *L. mutabilis* and cannot have been examined very carefully.

Folkmanova (1949) pointed out that many of the infraspecific forms of *L. mutabilis* enumerated and keyed by Verhoeff (1935) are based on unstable characters and are therefore without validity. Of Koch's specimens, the single male from the Tyrol is quite without posterior projections on T. 11 and 13 and agrees in other respects with Verhoeff's definition of *L. mutabilis mutabilis;* but all his other specimens including the lectotype have at least traces of posterior projections on T.11 and small but quite distinct projections on T.13, and would therefore run to *L. mutabilis* var. *carpathicus* in Verhoeff's key.

Although *L. mutabilis* and *L. pelidnus* are both fairly adequately described by Latzel (1880), the best descriptions of these two species, which are accompanied by illustrations of the male 15th legs upon which their differentiation largely depends, are those of Matic (1966).

41. ***Lithobius cinnamomeus*** L. Koch

Lithobius cinnamomeus L. Koch, 1862 : 77, fig. 35.

Type locality. Germany.

Material examined. "Lithobius cinnamomeus L.K." "Happurg [Franconian Jura]" B.M.(N.H.) Reg. no. 13.6.18.60–63. Two males and two females, all either 4th post-larval stadia or small adults of *L. muticus*.

Type specimens. The original description of *L. cinnamomeus* was based on a number of specimens of both sexes and all the above examples of *L. muticus* definitely belong to the syntypical series.

Remarks. As well as describing this form as being smaller, paler, and with fewer antennal articles and fewer ocelli than *L. muticus*, Koch noted the incurved internal pair of spurs on the female gonopods which he contrasted with the straight spurs

which he believed, mistakenly as we have seen, to occur in *L. muticus* (see p. 117). Although he made no mention of the swelling on the male 14th tibia in his description, he did confirm its presence in *L. cinnamomeus* in private correspondence with Latzel (Latzel, 1880 : 119). Latzel proposed *L. cinnamomeus* as a possible synonym of *L. muticus* but he remarked on the large head of the latter compared with the relatively small head of the former, and suggested that the two might possibly prove to be distinct species. But it is only in the largest males of *L. muticus* that the shape of the cephalic shield is really distinctive and there is no doubt that *L. cinnamomeus* is a synonym of *L. muticus*.

42. ***Lithobius lucifugus*** L. Koch

Fig. 5

Lithobius lucifugus L. Koch, 1862 : 82, fig. 38.

TYPE LOCALITY. Bolzano, Italy.

MATERIAL EXAMINED. "L. lucifugus [rewritten]" "Botzen [Bolzano]" B.M.(N.H.) Reg. no. 13.6.18.369. A single male 15 mm long with circular coxal pores.

"L. lucifugus [rewritten]" "Ratzes [Rasa, Italy], [leg.] Milde" B.M.(N.H.) Reg. no. 13.6.18.370. A female of *L. pelidnus*.

"lucifugus?, Nurnberg" B.M.(N.H.) Reg. no. 13.6.18.371. A male 3rd post-larval stadium of *L. mutabilis*.

"L. lucifugus? cinnamomeus? Tirol [rewritten]" B.M.(N.H.) Reg. no. 13.6.18.372. Two males and three females of *L. lucifugus*.

TYPE SPECIMEN. The original description of *L. lucifugus* was based on a single male and agrees exactly with the above male from Bolzano which is undoubtedly the holotype.

REMARKS. The circular coxal pores of the holotype explain why *L. lucifugus* is so far removed, in Koch's system, from *L. alpinus* and *L. granulatus* with which it is conspecific (see p. 130). The prosternum of the holotype (Fig. 5) with 2 + 2 teeth establishes this number of teeth as typical, but the appearance of 2 + 3 prosternal teeth on one of the specimens from the Tyrol is evidence of their variability in *L. lucifugus*. Koch's inclusion of a female of *L. pelidnus* under *L. lucifugus* is a further example of the mistakes he made in placing females of similar species.

L. lucifugus was fully described by Latzel (1880 : 120) and Brolemann (1930).

43. ***Lithobius lubricus*** L. Koch

Lithobius lubricus L. Koch, 1862 : 86, fig. 41.

TYPE LOCALITY. Nuremberg district.

MATERIAL EXAMINED. "L. lubricus [rewritten]" "fränk. Jura" B.M.(N.H.) Reg. no. 13.6.18.373–374. Three post-larval stadia of *L. calcaratus*, one belonging to the 1st, a male to the 2nd and a female to the 3rd.

"L. lubricus [rewritten]" "Dietenhofen [Franconian Jura]" B.M.(N.H.) Reg. no. 13.6.18.375. A male 3rd post-larval stadium of *L. calcaratus*.

"L. lubricus [rewritten]" "Gritz [Grütz, near Nuremberg], [hab.] Valzn. Weiher, Glaishammer" B.M.(N.H.) Reg. no. 13.6.18.376–379. Four post-larval stadia of *L. calcaratus*, one belonging to the 1st, and two males and a female to the 3rd.

TYPE SPECIMENS. The original description of *L. lubricus* was based on a number of specimens of both sexes. All the above examples of *L. calcaratus* come from the neighbourhood of Nuremberg and seem to belong to the syntypical series.

REMARKS. Koch's failure to identify these specimens as *L. calcaratus* is easily understood, as the characteristic femoral process on the male 15th leg does not become obvious during the development of this species until the 4th post-larval stadium (see p. 109). Synonymy of *L. lubricus* with *L. calcaratus* was first proposed by Stuxberg (1871) and has never been disputed.

44. ***Lithobius carinatus*** L. Koch

Fig. 6

Lithobius carinatus L. Koch, 1862 : 87, fig. 42.

TYPE LOCALITY. Greece.

MATERIAL EXAMINED. "Lithobius carinatus L.K." "Griechenland" B.M.(N.H.) Reg. no. 13.6.18.56–58. Three imperfectly cleared males with the antennae and all the legs missing.

"Lithobius carinatus L.K." "Patria?" B.M.(N.H.) Reg. no. 13.6.18.59. A single well-preserved male.

TYPE SPECIMENS. The original description of *L. carinatus* was based on a number of males. The above specimens from Greece seem to constitute the syntypical series and must have been examined by Koch before they lost their appendages. One of them, a male 24 mm long, is here formally designated as the lectotype (B.M.(N.H.) 13.6.18.56).

REMARKS. All the above specimens as well as Koch's description are clearly referable to the common Greek species known as *L. macrops* Karsch, 1888. Although this description is quite adequate it has been overlooked by most authors: only Attems (1926) has recognized *L. carinatus* as the correct name for *L. macrops*.

The striking difference between the relatively dense setae on the 15th prefemur and femur, and the very much sparser setae on the corresponding tibia, tarsus and metatarsus which Koch described, cannot be confirmed in the type specimens owing to their mutilation, but is present in the male from an unknown locality. However, three males and a female of this species (B.M.(N.H.) Reg. no. 89.3.29.36–38) from Athens, the type locality of *L. macrops*, are variable in respect of this character: one male and the female are similar to Koch's specimens but with more setae at the base of the 15th tibia, whereas the other two males have setae of much the same density on all the articles of the 15th legs: none of these specimens from Athens shows the

sharp difference between the setae of the femur and tibia which is so striking in Koch's specimen. It would, in fact, be quite reasonable to regard *L. carinatus* and *L. macrops* as subspecifically distinct if we knew the exact localities in Greece attaching to *L. carinatus* and if it were not for other specimens of the species (B.M.(N.H.) Reg. nos. 1905.8.24.77 and 03.8.25.23–25) from unknown localities in Greece showing various degrees of differentiation between the more setose proximal and the almost glabrous distal articles of the 15th legs. Further, Matic figured a specimen of *L. macrops* from Athens with a glabrous 15th metatarsus (Matic *et al.*, 1968: fig. 1B). *L. carinatus* should, therefore be regarded as the senior synonym of *L. macrops*.

Although this is an abundant and distinctive species the only really full account in the literature is that of Matic (Matic *et al.*, 1968), and because Koch's specimens differ in detail from that account they are described below. The characters of the appendages are taken from the specimens from an unknown locality.

Description. *Size:* 20 to 25 mm long and about 2·5 mm broad at T.10. *Colour:* dull yellow. *Head:* broader than long. *Antennae:* one-third of body-length; of 32 irregular articles, some broader than long, others slightly elongate, appearing only very sparsely setose although many of the setae may have been lost. *Ocelli:* a large posterior ocellus, an intermediate ocellus of much the same size and two much smaller anterior ocelli, exactly as figured by Matic (Matic *et al.*, 1968: fig. 1E); organ of Tömösvary rather smaller than smallest ocellus. *Prosternum:* with 2 + 2 teeth and a pair of lateral spines; lateral to the lateral spine the anterior border forms a narrow but distinct shoulder, sometimes amounting to a rounded node (Fig. 6). *Tergites:* the posterior angles of the large tergites all rounded, those of T.9 obtuse, those of T.11 right-angled and those of T.13 very slightly produced; T.14 relatively broad; intermediate tergite (T.16) truncate. *Sternites:* S.5 to S.15 beset with minute setae; many of these setae have been lost but their insertions are visible. *Coxal pores:* 4, 3, 3, 3; circular; the medial pore on the 12th coxa is much smaller than the others and may be hidden by the adjacent sternite. *Legs:* the 14th and 15th short and stout, less than one-third of body-length; 15th prefemur and femur densely setose; the three distal articles of the 15th leg almost glabrous; setae of the 14th leg arranged in much the same way as on the 15th, but their differentiation is less marked; two ventral rows of stout seriate setae on the 1st to 13th metatarsi, extending onto part of the adjacent tarsus in some legs; 15th accessory apical claw about two-fifths of length of the principal claw which is short and stout. *Gonopods*: of a single article.

Spinulation:

	Ventral					Dorsal				
	C	t	P	F	T	C	t	P	F	T
14	—	m	amp	amp	am	—	—	mp	p	p
15	—	m	amp	am	—	—	—	p	p	—

No coxolateral spines. All spines rather short and stout. Koch recorded a third ventral spine on the 15th femur and a single ventral spine on the 15th tibia.

45. ***Lithobius pubescens*** L. Koch

Lithobius pubescens L. Koch, 1867 : 898.

TYPE LOCALITY. Tinos, Aegean Archipelago.

MATERIAL EXAMINED. "L. pubescens [rewritten]" "Tinos Erber" B.M.(N.H.) Reg. no. 13.6.18.580. A male of *L. carinatus* 18 mm long.

"L. pubescens [rewritten]" "Syra Erber" B.M.(N.H.) Reg. no. 13.6.18.581–582. A male and a female of *L. carinatus* 16 mm and 12 mm long respectively.

"L. pubescens [rewritten]" "Smyrna Erber" "181 [printed]" B.M.(N.H.) Reg. no. 13.6.18.583–585. A male and two females of *L. carinatus* 16 to 19 mm long.

TYPE SPECIMEN. The original description of *L. pubescens* was based on a male and a female. The latter has not been found but the above male of *L. carinatus* from Tinos agrees exactly with the description and is here formally designated as the lectotype.

REMARKS. Although Koch made no comparsion between *L. pubescens* and *L. carinatus*, his brief description of the former is quite clear and Karsch (1888) remarked on the similarity between *L. pubescens* and *L. macrops* (= *carinatus*). The principal features which seem to have led Koch to describe *L. pubescens* as a distinct species are, as its name implies, the strongly setose antennae and 15th legs and the numerous minute setae on the posterior sternites of the male. The distal articles of the legs, particularly those of the 14th and 15th, of the lectotype and the specimens from Syria and Smyrna are certainly more densely setose than those of the Greek specimens of *L. carinatus*, but there is little true difference between the two groups of specimens in the setation of the antennae and the extent and density of the sternal setae. Most of these setae have been lost in Koch's specimens of *L. carinatus* and may not have been present even when he examined them originally. There would, in fact, be little reason for regarding *pubescens* as distinct from *carinatus* were it not for a marked difference in size.

Of the published figures for the lengths of Greek specimens, Karsch (1888) gave 23 mm, Verhoeff (1899) gave 20·5 to 21·5 mm and Matic (Matic *et al.*, 1968) gave 22 to 30 mm; Koch's specimens of *L. carinatus* are 20 to 25 mm and the other adult Greek specimens in the British Museum (N.H.) already referred to are 21 to 25 mm long; two smaller females (B.M.(N.H.) 03.8.25.24.and 25) from Greece are 13 mm and 14 mm long but they are obviously immature with 3, 3/2, 2, 2 coxal pores and only 2 + 2 very unequal spurs on the gonopods. Comparable figures for the lengths of specimens from Asia Minor and the Levant are that of Porat (1894) for a Syrian specimen (15 mm) and those of Verhoeff (1925, 1941, 1943) for specimens from Jaffa (13 to 14 mm), the Taurus Mountains (15 mm) and Alexandretta (19 mm); and of Koch's specimens of *L. pubescens*, the lengths of which have already been given, the female from Syria only 12 mm long seems to be mature with 4, 3, 3, 3 coxal pores and fully developed gonopods with 3 + 3 spurs.

There seems, therefore, to be some justification for retaining the name *pubescens* for a subspecies of *L. carinatus* occurring in the Aegean Archipelago, Asia Minor and the Levant and differing from the nominate subspecies in being less than 20 mm long

with the tarsi and metatarsi of the legs, particularly those of the 14th and 15th, more strongly setose.

46. ***Lithobius litoralis*** L. Koch

Lithobius litoralis L. Koch, 1867 : 899.

TYPE LOCALITY. Tinos, Aegean Archipelago.

TYPE SPECIMEN. The holotype. B.M.(N.H.) Reg. no. 13.6.18.368.

REMARKS. This species has been discussed in a previous publication (Eason, 1970a) in which it was shown to be a valid species of *Eupolybothrus* Verhoeff and not a synonym of *E. fasciatus* (Newport) as was previously supposed.

47. ***Lithobius nigripalpis*** L. Koch

Lithobius nigripalpis L. Koch, 1867 : 899.

TYPE LOCALITY. Tinos, Aegean Archipelago.

MATERIAL EXAMINED. "L. nigripalpis [rewritten]" "Tinos Erber" B.M.(N.H.) Reg. no. 13.6.18.575. A single male.

TYPE SPECIMEN. The original description of *L. nigripalpis* was based on a single male and agrees fairly well with the above specimen which is undoubtedly the holotype.

REMARKS. There has been uncertainty about the identity of this species ever since Verhoeff (1899) redescribed it as a subspecies of *L. forficatus* with either a simple apical claw on the 15th leg or with only a minute accessory claw. In subsequent keys and brief accounts (Verhoeff, 1925, 1937 etc.) the 15th legs of *L. nigripalpis* have always been described as having a simple claw. In fact, not only the holotype but also three specimens (a male and two females) from the Verhoeff Collection in the British Museum (N.H.) labelled "*Lithobius forficatus nigripalpis* Koch, Greece" (Reg. no. 03.8.25.64-66) all have small but distinct 15th accessory apical claws, and there is no doubt that all four specimens belong to *L. bulgaricus* Verhoeff, 1925, which thus becomes a junior synonym of *L. nigripalpis*. It may be that when he wrote his account of *bulgaricus*, Verhoeff had already sold his material belonging to *nigripalpis* to various museums and had no specimens available for re-examination; otherwise he would hardly have described *L. bulgaricus* as distinct.

Having decided that *L. nigripalpis* is identical with *L. bulgaricus* it remains to arrive at its taxonomic status. It clearly belongs to the *piceus-peregrinus* group of species and, contrary to Verhoeff's mistaken conception of the form as having close affinity with *L. forficatus*, most authors have regarded it as no more than a variety or even a synonym of one of the species of this group. Latzel (1880 : 65) included *L. nigripalpis* among the doubtful synonyms of *L. piceus*; Attems (1905) regarded *L. nigripalpis* and *L. peregrinus* as varieties of the same species; and Muralwitsch (1926) believed *L. forficatus nigripalpis* of Verhoeff to be identical with *L. viriatus* Sseliwanoff, 1880, another member of the *piceus-peregrinus* group.

Although Matic (1964) proposed *nigripalpis* as a variety of *L. bulgaricus*, he has recently (Matic, 1966; Matic & Darabantu, 1968) listed *L. nigripalpis* among the synonyms of *L. piceus* and described *L. bulgaricus* separately.

L. bulgaricus was originally described as a subspecies of *L. piceus* (Verhoeff, 1925) but Matic (1966) found these two forms to be sympatric in parts of Rumania so they can hardly belong to the same species. *L. nigripalpis* is, in fact, closer to *L. peregrinus* than to *L. piceus* but the absence of a prosternal diastema and the absence of denticles on the claw of the female gonopod (both of which are present in *L. peregrinus*) are sufficient grounds for regarding it as a true species.

The original record from Tinos, Verhoeff's (1899) records from the island of Aegina in the Saronic Gulf and the adjacent mainland of Attica (probably based partly on the specimens B.M.(N.H.) Reg. no. 03.8.25.64–66), Verhoeff's (1925) original record of *L. bulgaricus* from Ruschuk on the Danube, and the distribution Matic (1966) gave for *L. bulgaricus* show this species to be widespread in the eastern and southern Balkans as well as in the Aegean Archipelago. Records of *L. piceus olympicus* Verhoeff from the south Marmoran coast (Verhoeff, 1944), and of *L. politicus* Chamberlin from southwest Anatolia (Chamberlin, 1952), both probably refer to *L. nigripalpis* and suggest that the species is also widespread in Asia Minor. Attem's (1905) description of *L. peregrinus* from Erdschias-Dagh (Asia Minor) and Verhoeff's (1944) description of what he regarded as the true *L. nigripalpis* from Ankara must both have been based on specimens of *nigripalpis* in which the 15th accessory apical claw was either absent or so small as to be overlooked.

The only really full account of this species in the literature is that of Matic (1966) under *L. bulgaricus*. Because the holotype appears to be a pseudomaturus and therefore different in detail from Matic's account it is described below.

DESCRIPTION. *Length:* 19 mm. *Colour:* dark brown. *Antennae:* 8 mm long; of 48 articles. *Ocelli:* 1 + 4, 3, 2. *Prosternum:* with 4 + 4 teeth and the lateral spines lateral to the external teeth. *Tergites:* the posterior angles of T.8 and 10 rounded, those of T.12 blunt, those of T.14 angulated; posterior angles of T.9, 11 and 13 with prominent projections, those of T.13 being very long and sharp; posterior border of intermediate tergite strongly emarginate; the shape of the tergites is in marked contrast to that in *L. piceus* in which the posterior angles of T.10, 12 and 14 are sharp and slightly projecting. *Coxal pores*: 5, 5, 5, 4; circular. *15th legs:* 7 mm long; stout; a feeble external sulcus on prefemur, femur and tibia; accessory apical claw about a quarter the length of principal claw.

Spinulation:

	Ventral					Dorsal				
	C	t	P	F	T	C	t	P	F	T
1	—	—	mp	amp	am	—	—	mp	a–p	a
2	—	—	mp	amp	am	—	—	amp	a–p	a–p
3	—	—	mp	amp	am	—	—	amp	a–p	a–p
4	—	—	mp	amp	am	—	—	amp	a–p	a–p
5	—	—	mp	amp	am	—	—	amp	a–p	a–p
6	—	—	mp	amp	am	—	—	amp	a–p	a–p
7	—	—	amp	amp	am	—	—	amp	a–p	a–p

Spinulation:

	Ventral					Dorsal				
	C	t	P	F	T	C	t	P	F	T
8	—	—	amp	amp	am	—	—	amp	a–p	a–p
9	—	—	amp	amp	am	—	—	amp	a–p	a–p
10	—	—	amp	amp	am	a	—	amp	a–p	a–p
11	—	—	amp	amp	am	a	—	amp	a–p	a–p
12	—	—	amp	amp	am	a	—	amp	a–p	a–p
13	a	m	amp	amp	am	a	—	amp	p	a–p
14	a	m	amp	amp	am	a	—	amp	p	p
15	a	m	amp	amp	a	a	—	amp	p	—

15 VaC is duplicated on the right leg.

48. ***Lithobius asperatus*** L. Koch

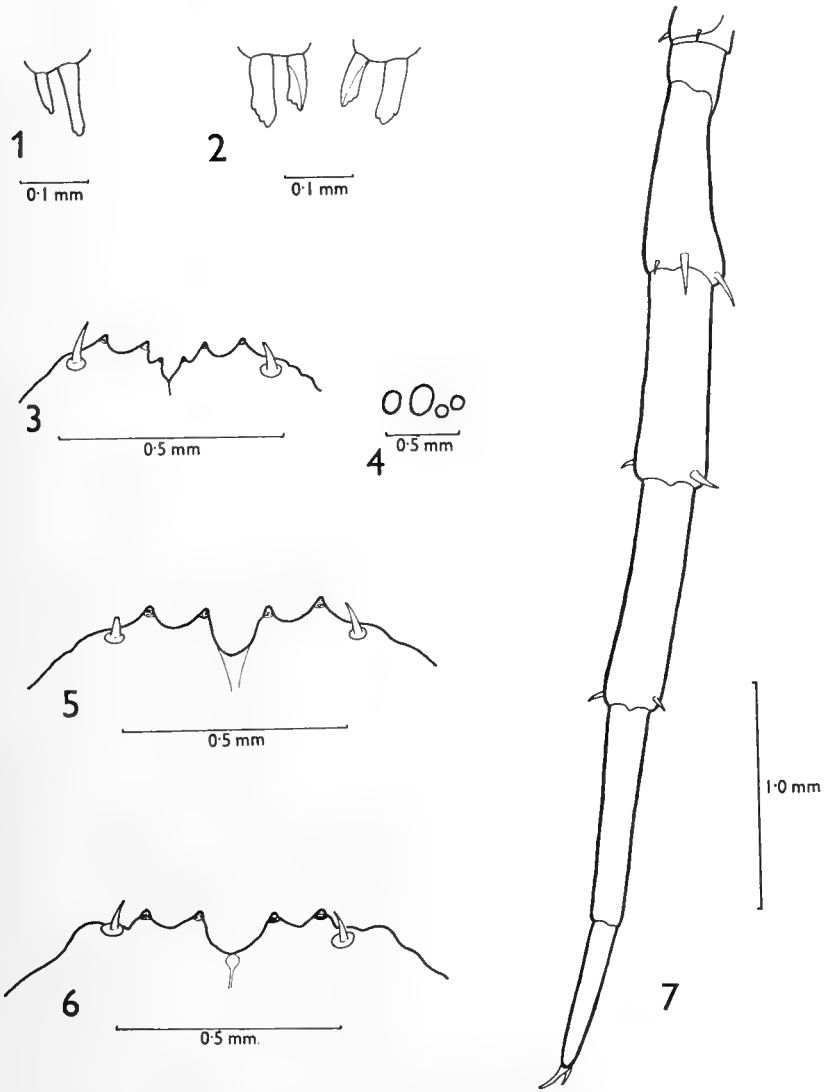
Lithobius asperatus L. Koch, 1878 : 788.

Type locality. Japan.

Remarks. *L. asperatus* was originally described from specimens belonging to a collection made by Dr. Albrecht von Roretz which has not been traced. There is, however, no doubt as to the identity of this species which is very common in Japan and much of eastern Asia and whose life-history has been studied in as much detail as that of any species of Lithobiidae (Murakami, 1958).

L. asperatus has been redescribed by Haase (1887) from the Phillipines and by Attems (1909) from Japan. Chamberlin (1920) considered that Attem's description, which gave 13 ocelli (Koch gave 23, Haase gave 19 to 23) and a ventral spine on the 15th tibia (neither Koch nor Haase gave this spine), applied to another species with fewer ocelli and more spines which he named *Bothropolys spinosior* on the basis of Attem's description. But specimens in the British Museum (N.H.) from Japan (Reg no. 1937.9.9.55) and southeast Korea (Reg. no. 93.3.27.6) have 24 and 22 ocelli respectively and in both, the spinulation of the 14th and 15th legs is exactly as described by Attems: there is therefore no correlation between the number of ocelli and the spinulation, and *B. spinosior* is not a valid species. Another of Attem's descriptions of *L. asperatus*, based on a single male from the Hawaiian Islands (Attems, 1903), was questioned by Chamberlin (1920) with more justification: this Hawaiian specimen had very deficient spinulation compared with the typical *L. asperatus* and Attems himself had already referred it to a separate species, *Bothropolys maluhianus* (Attems 1914): but Chamberlin, who cannot have read Attem's later paper, renamed it *B. oahuanus*.

L. asperatus belongs to the genus *Bothropolys* Wood as emended by Chamberlin (1925a) who divided the genus into *Bothropolys* s.str. and *Poropolys*, the former with and the latter without posterior projections on T.6 and 7. In *B. asperatus* the projections on T.6 are very feeble and were not even mentioned by Koch in his original description, while those on T.7, though distinct in some specimens, are so feeble in the example from Japan in the British Museum (N.H.) that one cannot say to which of Chamberlin's subgenera it belongs: *Poropolys* should therefore be disregarded.



FIGS 1–7. Fig. 1. *L. agilis*, spurs of left gonopod of neotype, ventral. Fig. 2. *L. erythrocephalus*, spurs of gonopods of neotype, ventral. Fig. 3. *L. alpinus*, dental margin of prosternum of holotype, ventral. Fig. 4. *L. sulcatus*, ocelli of lectotype. Fig. 5. *L. lucifugus*, dental margin of prosternum of holotype, ventral. Fig. 6. *L. carinatus*, dental margin of prosternum of lectotype, ventral. Fig. 7. *L. piceus*, left 15th leg of female (Franconian Jura), dorsal.

TABLE I

Nominal species	Date	Type locality as published	Designate type material	Validity and status	Generic classification
aeruginosus L.K.	1862	Nuremberg district	Lectotype (Franconian Jura)	valid	*Lithobius* (*Monotarsobius*)
agilis C.L.K.	1847	Bavaria	Neotype (Mögeldorf [Nuremberg])	valid	*Lithobius* s. str.
alpinus L.K.	1862	Seiseralpe [Italian Tyrol]	Holotype	non *L. alpinus* Heer, 1845 = *L. lucifugus* var. *latzeli* Verhoeff, 1935, Syn. nov.	
asperatus L.K.	1878	Japan	—	valid	*Bothropolys*
bucculentus L.K.	1862	Munich district	—	= *L. tricuspis* Meinert, 1872. Syn. nov. (see p. 126)	
calcaratus C.L.K.	1844	Germany	Neotype (Nuremberg)	valid	*Lithobius* s. str.
carinatus L.K.	1862	Greece	Lectotype	valid = *L. macrops* Karsch, 1888	*Lithobius* s. str.
cinnamomeus L.K.	1862	Germany	Syntypes (Happurg [Franconian Jura])	= *L. muticus* C. L. Koch, 1847	
communis C.L.K.	1844	Germany	—	= *L. mutabilis* L. Koch, 1862 (see p. 110)	
coriaceus L.K.	1862	Germany	Syntypes (Franconian Jura)	= *L. forficatus* (Linn. 1758)	
crassipes L.K.	1862	Nuremberg district	Lectotype (Franconian Jura)	valid	*Lithobius* (*Monotarsobius*)
curtipes C.L.K.	1847	Bavaria	Neotype (Nuremberg)	valid = *L.* (*Monotarobsius*) *baloghi* Loksa, 1947. Syn. nov.	*Lithobius* (*Monotarsobius*)
dentatus C.L.K.	1844	Germany	Neotype (Nuremberg district)	valid	*Lithobius* s. str.
erythrocephalus C.L.K.	1847	Bavaria	Neotype (Happurg [Franconian Jura])	valid	*Lithobius* s. str.
festivus L.K.	1862	Garmisch [Bavaria]	Syntype	= *Eupolybothrus grossipes* (C. L. Koch, 1847)	

Nominal species	Date	Type locality as published	Designate type material	Validity and status	Generic classification
forficatus var. *villosus* L.K.	1862	Bavarian Alps	Holotype	= *L. forficatus*	
fossor L.K.	1862	Grütz (near Nuremberg); Ehrenbürg [Franconian Jura]	Syntypes	= *L. piceus* L. Koch, 1862	
glabratus C.L.K.	1847	Bavaria	—	= *L. melanops* Newport, 1845	
granulatus L.K.	1862	Unknown	Holotype	= *L. lucifugus* L. Koch, 1862. Syn. nov.	
grossipes C.L.K.	1847	Triest	Holotype (Idrija [Yougoslavia])	valid	*Eupolybothrus* s. str.
hortensis L.K.	1862	Nuremberg; Landstuhl (Rhineland Palinate)	Syntypes	= *L. forficatus*	
immutabilis L.K.	1862	Germany	Syntypes (Nuremberg)	= *L. dentatus* C. L. Koch, 1844	
impressus C.L.K.	1841	Algerian coast	—	valid	*Eupolybothrus* (*Allopolybothrus*)
inermis L.K.	1856	Malaga [Spain]	—	valid	*Lithobius* s. str.
litoralis L.K.	1867	Tinos [Aegean Archipelago]	Holotype	valid	*Eupolybothrus* s. str.
lubricus L.K.	1862	Nuremberg district	Syntypes	= *L. calcaratus* C. L. Koch 1844	
lucifugus L.K.	1862	Bolzano [Italy]	Holotype	valid	*Lithobius* s. str.
macilentus L.K.	1862	Nuremberg; Franconian Jura; Bolzano [Italy]	Lectotype (Grütz [Nuremberg])	valid = *L. aulacopus* Latzel, 1880 Syn. nov.	*Lithobius* s. str.
melanocephalus C.L.K.	1862	Ehrenbürg (Franconian Jura)	Syntypes	= *L. melanops*	
minimus L.K.	1862	Germany	—	*nomen dubium*	
minutus C.L.K.	1847	Bavaria	—	= *L. mutabilis* (see p. 118)	
montanus C.L.K.	1847	South Tyrol	—	= *Eupolybothrus grossipes*	
mordax L.K.	1862	New Orleans [U.S.A.]	—	valid	*Neolithobius*

Nominal species	Date	Type locality as published	Designate type material	Validity and status	Generic classification
muscorum L.K.	1862	Germany	Holotype	= *L. forficatus*	
mutabilis L.K.	1862	Germany	Lectotype (Franconian Jura)	valid	*Lithobius* s. str.
muticus C.L.K.	1847	Bavaria	Neotype (Franconian Jura)	valid	*Lithobius* s. str.
nigripalpis L.K.	1867	Tinos [Aegean Archipelago]	Holotype	valid = *L. piceus bulgaricus* Verhoeff, 1925. Syn. nov.	*Lithobius* s. str.
parisiensis L.K.	1862	Paris	—	= *L. forficatus*	
piceus L.K.	1862	Garmisch [Bavaria]	—	valid	*Lithobius* s. str.
pubescens L.K.	1867	Tinos [Aegean Archipelago]	Lectotype	subspecies of *L. carinatus* L. Koch, 1862. Comb. nov.	
punctulatus C.L.K.	1847	Triest	—	*nomen dubium*	
sordidus L.K.	1862	Munich district	—	= *L. piceus*	
sulcatus L.K.	1862	Nuremberg	Lectotype (Grütz [Nuremberg])	valid = *L. microps*: Verhoeff, 1931? (non Meinert, 1868)	*Lithobius* (*Monotarsobius*)
transmarinus L.K.	1862	New Orleans [U.S.A.]	—	valid	*Neolithobius*
trilineatus L.K.	1862	Bahia [Brazil]	Syntype	= *L. forficatus*	
varius C.L.K.	1847	Bavaria	—	*nomen dubium*	
velox L.K.	1862	Landstuhl (Rhineland Palinate); Franconia; Vienna district	Syntypes	= *L. melanops*	
venator L.K.	1862	Ehrenbürg (Franconian Jura)	Holotype	= *L. melanops*	

ACKNOWLEDGEMENTS

My sincere thanks are due to the Trustees of the British Museum (N.H.) for lending me specimens; to Dr. G. O. Evans, Dr. J. G. Sheals and Mr. K. H. Hyatt of the Arachnida Section of the Department of Zoology of the Museum for their personal help; to the Zoological Museum, Berlin and Dr. M. Moritz for lending me specimens; and to Professor O. Kraus of the Zoological Museum, Hamburg and Dr. E. Popp of the Zoologische Staatssammlung, Munich for their help in tracing the history of the Koch and Keyserling Collections.

REFERENCES

ATTEMS, C. G. (1903). Beiträge zur Myriopodenkunde. *Zool. Jb.* (Syst.), **18** : 63–154.
—— (1904). Central und hoch-asiatische Myriopoden. *Zool. Jb.* (Syst.), **20** : 113–130.
—— (1905). Myriopoden. In *Ergebnisse einer naturwissenschaftlichen Reise zum Erdschias-Dagh* (*Kleinasien*). Penther, A. & Zederbauer, E. (eds.). *Annln naturh. Mus. Wien*, **20** : 163–167.
—— (1909). Die Myriopoden der Vega-Expedition. *Ark. Zool.* **5**(3) : 1–84.
—— (1914). Die indo-australischen Myriopoden. *Arch. Naturgesch.* **80,** Abt.A, 4 Heft : 1–398.
—— (1926). *Étude sur les Myriopodes recueillis par M. Henri Gadeau de Kerville pendant son voyage zoologique en Syrie* (*Avril–Juin* 1908). Rouen : imprimerie Lecerf.
—— (1927). Myriopoden aus dem nördlichen und östlichen Spanien, gesammelt von Dr. F. Haas in den Jahren 1914–1919. *Abh. senckenb. naturforsch. Ges.* **39** : 233–290.
—— (1929). Die Myriopodenfauna von Albanien und Jugoslavien. *Zool. Jb.* (Syst.), **56** : 269–356.
BOLLMAN, C. H. (1893). The Myriapoda of North America. *Bull. U.S. natn. Mus.* **46** : 1–210.
BOREK, V. (1967). Beitrag zur Kenntnis der Variabilität der Art *Lithobius lucifugus* L. Koch, 1862 (Chilopoda). *Věst. čsl. Spol. zool.* **31** : 109–115.
BROLEMANN, H. W. (1896). Liste de Myriapodes des États-Unis, et principalement de la Caroline du Nord. *Annls Soc. ent. Fr.* **65** : 43–70.
—— (1898). Myriapodes d'Ahusquay (Basses Pyrénées). *Feuille jeun. Nat.* (3) **28** : 200–203.
—— (1909) Os Myriapodos do Brazil. In *Catalogos da Fauna Brazileira* 2. São Paulo.
—— (1926). Myriapodes des Pyrénées-Orientales. *Bull. Soc. Hist. nat. Toulouse*, **54** : 233–267.
—— (1930). Myriapodes. Chilopodes. *Faune Fr.* **25** : 1–405.
CHAMBERLIN, R. V. (1911). The Lithobiomorpha of the Southern States. *Ann. ent. Soc. Am.* **4** : 32–50.
—— (1920). The Myriapoda of the Australian region. *Bull. Mus. comp. Zool. Harv.* **64** :1–269.
—— (1925a). The Ethopolidae of America north of Mexico. *Bull. Mus. comp. Zool. Harv.* **57** : 383–437.
—— (1925b). The genera *Lithobius, Neolithiobus, Gonibius* and *Zinapolys* in America north of Mexico. *Bull. Mus. comp. Zool. Harv.* **57** : 439–504.
—— (1952). On the Chilopoda of Turkey. *Istanb. Üniv. FenFak. Mecm.* (B)**17** : 183–258.
DALLA TORRE, K.-W. von (1882). Beiträge zur Arthropoden-Fauna Tirols. *Ber. naturw.-med. Ver. Innsbruck*, **12** : 32–73.
DEMANGE, J.-M. (1958). Sur quelques Myriapodes cavernicoles de France et de Suisse. *Revue suisse Zool.* **65** : 843–855.
DOBRORUKA, L. J. (1962). Über *Lithobius erythrocephalus* C. L. Koch, 1847 (Chilopoda). *Zool. Anz.* **168** : 43–45.
EASON, E. H. (1951). Notes on the Chilopoda (centipedes) of Warwickshire and Worcestershire. *Ann. Mag. nat. Hist.* (12)**4** : 257–268.
—— (1964). *Centipedes of the British Isles.* London: Warne.
—— (1965). On *Lithobius tricuspis* Meinert (Chilopoda, Lithobiidae) in Britain. *Ann. Mag. nat. Hist.* (13)**8** : 285–295.

EASON, E. H. (1970a). A redescription of the species of *Eupolybothrus* Verhoeff s.str. preserved in the British Museum (Natural History) and the Hope Department of Zoology, Oxford (Chilopoda, Lithobiomorpha). *Bull. Br. Mus. nat. Hist.* (Zool.) **19** : 289–310.

—— (1970b). The Chilopoda and Diplopoda of Iceland. *Entomologica scand.* **1** : 47–54.

—— (1971). The type specimens and identity of the species described in the genus *Lithobius* by George Newport in 1844, 1845 and 1849. *Bull. Br. Mus. nat. Hist.* (Zool.) **21** : 297-311

FEDRIZZI, G. (1877). I Litobi Italiani. *Atti Accad. scient. veneto-trent.-istriana,* **5**(2) : 184–233.

FOLKMANOVA, B. (1949). Subspecie druhu *Lithobius mutabilis* Koch v našich zemích. *Věst. čsl. zool. Spol.,* **13** : 56–68.

—— (1951). O některých Chilopodech nových pro Moravü. *Sb. Klubu přír. Brně,* **29** : 98–104.

—— (1954). Přispěvek k poznáni slezskych stonožek z Beskyd. *Přírodov. Sb. ostrav. Kraje,* **15** : 194–219.

FOLKMANOVA, B. & LANG, J. (1955). Stonožky vrchu Kotouce u Stramberka. *Přírodov. S. ostrav. Kraje,* **16** : 506–512.

—— (1960). Přispěvek k poznáni stonožek Rychlebských hor. *Přírodov. Cas. slezský,* **21** : 355–372.

GARBOWSKI, T. (1879) Phyletische Deutung der Lithobiusformen. *Zool. Jb.* (Syst.), **9** : 244–270.

GERVAIS, M. P. (1837). Études pour servir a l'histoire naturelle des Myriapodes. *Annls Sci. nat.* Zool., (2)**7** : 35–60.

HAASE, E. (1880). *Schlesiens Chilopoden; 1. Chilopoda anamorpha.* Inaugural-Dissertation. Breslau: A. Neumann.

—— (1887). Die Indisch-Australischen Myriopoden; 1. Chilopoden. *Abh. Ber. K. zool. anthrop.-ethn. Mus. Dresden,* **1**(5) : 1–118.

HEER, O. (1845). Ueber die obersten Gränzen des Thierischen und Pflanzlichen lebens in unseren Alpen. *Zürch. Jug. naturf. Ges. Zürich,* **47** : 1–19.

JEEKEL, C. A. W. (1964). Beitrag zur Kenntnis der Systematik und Ökologie der Hundertfüsser (Chilopoda) Nordwestdeutschlands. *Abh. Verh. naturw. Ver. Hamburg,* N.F.**8** : 111–153.

—— (1967). On two Italian *Lithobius* species described by Silvestri, with taxonomic notes on the genus *Eupolybothrus* Verhoeff (Chilopoda, Lithobiidae). *Beaufortia,* **14** : 165–175.

KARSCH, F. (1888). Verzeichniss der von Herrn. E. v. Oertzen in den Jahren 1884–1885 in Griechenland und auf Kreta gesammelten Myriopoden. *Berl. ent. Z.* **32** : 220–224.

KOCH, C. (1910). *Die von Dr. Ludwig Koch in Nürnberg hinterlassene Arachniden – und Myriapoden – Sammlung.* Nürnberg: J. L. Stich.

KOCH, C. L. (1841). Arachnida und Myriapoda. In *Wagner's Reisen in der Regentschaft Algier* 3. Leipzig.

—— (1844). *Deutchlands Crustaceen, Myriapoden und Arachniden* 40. Regensburg.

—— (1847). System der Myriapoden. In *Kritische Revision der Insectenfauna Deutschlands* 3. Panzer, G. & Herrich-Schäffer, A. (eds.). Regensburg.

—— (1863). *Die Myriapoden* 1 & 2. Halle: H. W. Schmidt.

KOCH, L. (1862). *Die Myriapodengattung* Lithobius. Nürnberg: J. L. Lotzbeck.

—— (1867). Zur Arachniden – und Myriapoden – Fauna süd-Europas. *Verh. zool. – bot. Ges. Wien,* **17** : 857–900.

—— (1878). Japanesische Arachniden und Myriapoden. *Verh. zool. – bot. Ges. Wien,* **27** : 735–797.

LATZEL, R. (1880). *Die Myriopoden der Österreichisch – Ungarischen Monarchie,* 1. *Die Chilopoden.* Wien : Holder.

LEACH, W. E. (1814). Crustaceology. In *Brewster's Edinburgh Encylcopaedia* 7. Edinburgh.

LÉGER, L. & DUBOSCQ, O. (1903). Recherches sur les Myriapodes Corse et leurs parasites. *Archs Zool. exp. gén.* (4)**1** : 307–358.

LIGNAU, N. G. (1914). Vielfüssler aus Abchasien. *Ezheg. zool. Muz.* **19** : 349–368.

LOHMANDER, H. (1957). Faunistiskt fältarbete I Nord-och Västjylland 1954 och 1956. *Årstr. Göteborgs naturhisto. Mus.,* **1957** : 29–86.

LOKSA, I. (1947). Beiträge zur Kenntnis der Steinläufer –, Lithobiiden – Fauna des Karpatenbeckens, 1. *Fragm. faun. hung.* **10** : 73–85.
—— (1948). Beiträge zur Kenntnis der Steinläufer– , Lithobiiden – Fauna des Karpatenbeckens, 2. *Fragm. faun. hung.* **11** : 1–11.
LUCAS, H. (1849). Histoire naturelle des animaux articulés. In *Exploration scientifique de l'Algerie pendant les années* 1840, 1841, 1842. Zoologie 1. Paris.
MATIC, Z. (1961). Chilopodi, specialmente cavernicoli, raccolti in Toscana da Paola e Benedetto Lanza e da Giorgio Marcucci. Nota II. *Monitore zool. ital.* **69** : 60–65.
—— (1964). Nota critica asupra unor specii de Lithobiidae (Chilopoda) din fauna Republicii Populare Romîne. *Studii. Cerc. Biol. Cluj*, Zool. **16** : 187–191.
—— (1966). Chilopoda : Anamorpha. In *Fauna Republicii Socialiste România*. 6 București.
MATIC, Z., CLICHICI, M. & DARABANTU, C. (1968). Contributio alla conoscenza dei Chilopodi di Grecia. *Boll. Sed. Accad. gioenia Sci. nat.* (4)**9** : 307–317.
MATIC, Z. & DARABANTU, C. (1968). Note critique sur quelques espèces du genre *Lithiobius* (Chilopoda, Lithobiidae). *Izv. zool. Inst. Sof.* 26 : 103–117.
MEINERT, F. (1868). Danmarks Scolopender og Lithobier. *Naturh. Tidsskr.* (3)**5** : 241–268.
—— (1872). Myriapoda Musaei Havniensis: bidrag til myriapodernes morphologi og systematik; II Lithobiini. *Naturh. Tidsskr.* (3)**8** : 281–344.
MURAKAMI, Y. (1958). The life-history of *Bothropolys asperatus* (L. Koch). *Zool. Mag. Tokyo*, **67** : 217–223. (in Japanese).
MURALEWITSCH, W. S. (1926). Übersicht über die Chilopodenfauna des Kaukasus. *Zool. Anz.* **69** : 27–44.
NEGREA, S. (1965). Contribution à l'étude de certains Lithobiidae (Chilopoda) des grottes de Roumanie. *Int. J. Speleol.* **1** : 287–305.
NEWPORT, G. (1845). Monograph of the class Myriapoda, order Chilopoda. *Trans. Linn. Soc. Lond.* **19** : 349–439.
POCOCK, R. I. (1890). Contributions to our knowledge of the Chilopoda of Liguria. *Annali Mus. civ. Stor. nat. Giacomo Doria*, **29** : 59–68.
PORAT, C. O. von (1869). Redogörelse för en under sommaren 1868 utford zoologisk resa till Skäne och Blekinge. *Öfvers. VetenskAkad. Förh. Stockh.* **26** : 631–653.
—— (1894). Myriapodes récoltés en Syrie par le Docteur Théodore Barrois. *Revue biol. N Fr.* **6** : 62–79.
ROSENHAUER, W. G. (1856). *Die Thiere Andalusiens*. Erlangen: T. Blaesing.
ROSICKY, F. V. (1876). Die Myriopoden Böhmens. *Arch. naturw. LandDurchforsch. Böhm.* **3,** Abt. 4, No. 7 : 1–44.
SAY, T. (1821). Descriptions of the Myriapoda of the United States. *J. Acad. nat. Sci. Philad.* **2** : 102–114.
SILVESTRI, F. (1897). Contributio alla conoscenza dei Chilopodi e Diplopodi della Sicilia. *Boll. Soc. ent. ital.* **29** : 233–261.
SSELIWANOFF, A. (1880). Materiali k izucheniyu russkikh tisyachenogikh. *Trudȳ russk. ént. Obshch.* **11** : 3–26.
STUXBERG, A. (1871). Bidrag till Skandinaviens Myriopodologi II. Sveriges Chilopoder. *Öfvers. VetenskAkad. Förh. Stockh.* **28** : 493–512.
—— (1876). Myriopoder från Sibirien och Waigatsch ön samlade under Nordenskiöldska expeditionen 1875. *Öfvers. VetenskAkad. Förh. Stockh.* **33**(2) : 11–38.
TOBIAS, D. (1969). Grundsätzliche Studien zur Art-Systematik der Lithobiidae (Chilopoda: Lithobiomorpha). *Abh. senckenb. naturforsch. Ges.* **523** : 1–51.
TROTZINA, A. (1893). Vier neue *Lithobius* – Arten aus Central-Asien. *Horae Soc. ent. Ross.* **28** : 247–253.
VERHOEFF, K. W. (1899). Beiträge zur Kenntniss paläarktischer Myriopoden. XI. Aufsatz: neue und wenig bekannte Lithobiiden. *Verh. zool. – bot. Ges. Wien*, **49** : 451–459.
—— (1905). Über die Entwicklungsstufen der Steinläufer, Lithobiiden, und Beiträge zur Kenntnis der Chilopoden. *Zool. Jb.* (Supplement), **8** : 195–298.

VERHOEFF, K. W. (1925). Beiträge zur Kenntnis der Steinläufer, Lithobiiden. *Arch. Naturgesch.* **91** : 124–158.
—— (1931). Chilopoden der Insel Elba. *Zool. Anz.* **95** : 302–312.
—— (1934). Beiträge zur Systematik und Geographie der Chilopoden. *Zool. Jb.* (Syst.), **66** : 1–112.
—— (1935). Quer durch Schwarzwald und schweizerischen Jura (Chiemgau), Chilopoden. *Verh. naturw. Ver. Karlsruhe*, **31** : 181–208.
—— (1937). Chilopoden – Studien. Zur Kenntnis der Lithobiiden. *Arch. Naturgesch.* N.F.**6** : 171–257.
——. (1941). Asyanin zoogeografiyasi ve hayvan sistematiğe hakkinda. Asiatische Beiträge. *Istanb. Üniv. FenFak. Mecm.* (B)**6** : 85–117.
—— (1943). Über Chilopoden der Türkei. III. Aufsatz. *Zool. Anz.*, **143** : 116–140.
——. (1944). Asya hayvanlari ve zoogeografiyasi hakkinda. Asiatische Beiträge VIII. Istanb. Üniv. *FenFak. Mecm.* (B)**9** : 307–347.

Dr. E. H. EASON
BOURTON FAR HILL
MORETON-IN-MARSH
GLOUCESTERSHIRE

A LIST OF SUPPLEMENTS TO THE ZOOLOGICAL SERIES OF THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY)

1. KAY, E. ALISON. Marine Molluscs in the Cuming Collection British Museum (Natural History) described by William Harper Pease. Pp. 96; 14 Plates. 1965. (Out of Print.) £3.75.
2. WHITEHEAD, P. J. P. The Clupeoid Fishes described by Lacepede, Cuvier and Valenciennes. Pp. 180; 11 Plates, 15 Text-figures. 1967. £4.
3. TAYLOR, J. D., KENNEDY, W. J. & HALL, A. The Shell Structure of Mineralogy at the Bivalvia. Introduction. Nuculacea-Trigonacea. Pp. 125; 29 Plates, 77 Text-figures. 1969. £4.50.
4. HAYNES, J. R. Cardigan Bay recent Foraminifera (Cruises of the R.V. *Antur*) 1962–1964. (*In press.*)

Printed in England by Staples Printers Limited at their Kettering, Northants, establishment

CONTRIBUTIONS TO THE LIFE-HISTORIES AND DEVELOPMENT OF *CUCULLANUS MINUTUS* RUDOLPHI, 1819 AND *C. HETEROCHROUS* RUDOLPHI, 1802 (NEMATODA : ASCARIDIDA)

D. I. GIBSON

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 22 No. 5
LONDON : 1972

CONTRIBUTIONS TO THE LIFE-HISTORIES AND DEVELOPMENT OF *CUCULLANUS MINUTUS* RUDOLPHI, 1819 AND *C. HETEROCHROUS* RUDOLPHI, 1802 (NEMATODA : ASCARIDIDA)

BY

DAVID IAN GIBSON

Pp 151–170; 3 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 22 No. 5
LONDON : 1972

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY) *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 22 *No.* 5 *of the Zoological series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation
Bull. Br. Mus. nat. Hist. (Zool.)

© Trustees of the British Museum (Natural History), 1972

TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 3 *March*, 1972 *Price* 70*p*

CONTRIBUTIONS TO THE LIFE-HISTORIES AND DEVELOPMENT OF *CUCULLANUS MINUTUS* RUDOLPHI, 1819 AND *C. HETEROCHROUS* RUDOLPHI, 1802 (NEMATODA : ASCARIDIDA)

By D. I. GIBSON

CONTENTS

		Page
1.	SYNOPSIS	153
2.	INTRODUCTION	153
3.	METHODS	154
4.	RESULTS AND DISCUSSION	155
	A. *Cucullanus minutus*	155
	(i) Larval and adult development	155
	(ii) Life-history	158
	(iii) Discussion	158
	B. *Cucullanus heterochrous*	161
	(i) Larval and adult development	161
	(ii) Life-history	164
	(iii) Discussion	164
5.	FINAL DISCUSSION	167
6.	ACKNOWLEDGEMENTS	168
7.	REFERENCES	168

1. SYNOPSIS

The larval stages of the nematodes *Cucullanus minutus* and *C. heterochrous* from the flounder *Platichthys flesus* (L.) are described, those of *C. heterochrous* have not been previously recorded.

Information on the incidence of infestation of flounders with these larvae throughout the year is used to make a significant contribution to our knowledge of the life-histories of these two species. The work also indicates that *C. minutus* and *C. heterochrous* are normally geographically isolated from each other, and that this is associated with temperature and their life-histories.

2. INTRODUCTION

Cucullanus minutus and *C. heterochrous* were two of the commonest nematodes found in the flounder *Platichthys flesus* (L). from the estuary of the River Ythan, Aberdeenshire and from the sea off Aberdeen during the course of a survey of its helminth parasites. From previous work on the species of this genus, it appeared that the most obvious topics worthy of investigation were their life-histories and,

especially in the case of *C. heterochrous*, the morphology of the larval stages. Janiszewska (1939) has described the third- and fourth-stage larvae of *C. minutus*, but did not determine any of this parasite's earlier life-history. With regard to *C. heterochrous*, no information on its life-history is available in the literature, and its larval stages do not appear to have been recorded previously. This is surprising considering how common and widespread these species are in flatfish.

A study of the literature revealed that there is little information on the life-histories of many members of the genus *Cucullanus*, and that no life-history has been satisfactorily explained throughout the complete cycle. The only explanation of a complete life-cycle is that of Vessichelli (1910) for *C. stelmioides* (Vessichelli, 1910). Vessichelli states that the eggs are laid and hatch in the gut-lumen of the lamprey *Petromyzon planeri* (Bloch). The larvae penetrate the gut-wall, encyst and remain there during the period of gut reduction before spawning. After spawning the lampreys perish, and lamprey larvae become infested by feeding upon the dead bodies of the adult lampreys. According to Shulman (1957) Vessichelli's work has not been confirmed and requires further investigation. Janiszewska (1939) showed that some of the larval stages of *C. minutus* were present in the gut-wall of flounders and that the final stage larvae migrated into the gut-lumen, but she could not ascertain how these larval stages came to be present in the gut-wall. Le-Van-Hoa & Pham-Ngoc-Khue (1967), when describing *C. chabaudi*, showed in the laboratory that the eggs of this species embryonate in two days, the first moult occurs inside the egg after four days and the second-stage larvae hatched from the eggs after five to six days. These authors then stated that the second-stage larvae continue to grow inside the swim-bladder of a fish (*Pangasius pangasius* Hamilton Buchanan), the second moult occurs in the liver, and the third and fourth larval stages are present in the gall-bladder and bile-duct. The fourth-stage larvae then migrate along the bile-duct to the intestine where the adult nematodes are found. These authors did not state how the second-stage infested the fish, and did not describe the larval stages. Finally, preliminary comments upon the life-histories of *C. minutus* and *C. heterochrous*, which are enlarged upon below, were made by MacKenzie & Gibson (1970).

3. METHODS

The mean incidence of infestation of the adult and larval stages of these two nematodes were obtained during a survey of the helminth parasites of the flounder. Seven hundred and forty flounders from the estuary of the River Ythan, Aberdeenshire (termed 'estuarine flounders') and one hundred and seventy flounders from the sea off Aberdeen (termed 'marine flounders') were examined. These results are represented in fig. 3. Most of the larvae were removed from the mucosa and sub-mucosa of the gut-wall by scraping, and the remainder deep in the sub-mucosa were found by examining sections of squashed gut-wall with transmitted light. The difference between mature and immature adult nematodes was taken to be, in the case of the females, the presence or absence of eggs, and, in the case of

the males, the presence of clearly defined spicules when viewed under a low powered (× 10) microscope; but in most cases the mature and immature could easily be distinguished by size.

In the hatching experiments the adult worms were removed from the host, left over-night in 40% seawater, and the eggs produced were removed and kept in 80% seawater in a solid watch-glass.

4. RESULTS AND DISCUSSION

A. *Cucullanus minutus*

The only previous work on the life-history of this species was done by Janiszewska (1939) who described in detail the larval stages recovered from the gut-wall of flounders from the Baltic Sea. The free-living larvae have, however, never been described.

(i) Larval and adult development.

a. The egg:

Length : 61–68 μm
Breadth : 34–38 μm

The eggs were prolate spheroids and contained an unsegmented ovum when they left the female. The ova were seen to cleave into two- and four-cell stages, and then after two days the morula and blastula stages were visible. After four days a nematode larva was visible, coiled and moving within the egg-shell, but hatching did not take place until about seven days at 19°C. (133 degree days). Embryonation was very slow at low temperatures and was not observed below 7°C.

b. The first- and second-stage larvae:

Length : 304–374 μm
Breadth : 13 μm

The free-living larvae which hatched from the eggs (fig. 1) may have been the first- or second-stage larvae. No sign of a moulted cuticle was visible around the hatched larvae, though if such a cuticle had been tight fitting it may have been present. If this species resembles *C. chabaudi* (Le-Van-Hoa & Pham-Ngoc-Khue, 1967) then the first moult occurs within the egg, or if it resembles *C. heterochrous* (see below) the first larval cuticle is probably not lost until several days have passed in the free-living stage. Either way it is probable that the first- and second-stage larvae are very similar in appearance. Very little of the internal anatomy of these larvae was visible, though the anterior part of the oesophagus could be seen, showing that it was poorly developed compared with the adult. The remainder of the larva was obscured by the nuclei which, at this stage, are tightly packed together. These larvae were very active and capable of swimming. Unlike *C. chabaudi*, no second-stage larvae were ever recovered from the fish host.

c. The third-stage larva (fig. 1):

Length :	600–1,237 μm
Breadth :	40–80 μm
Oesophagus :	245–306 μm
Tail :	71–106 μm

This stage was described in detail by Janiszewska (1939) as the first larval stage from the intestinal wall. These larvae were situated in the mucosa and sub-mucosa of mainly the anterior intestine. The anatomy of this stage was as described by Janiszewska (1939), except that I believe that the thickening of the cuticle on the lips close to the mouth might in fact act as a boring tooth similar to that in the infestive stages of some anisakine nematodes.

d. The fourth-stage larva (figs 1 & 2):

Length :	720–1,210 μm
Breadth :	58–100 μm
Oesophagus :	278–346 μm
Tail :	80–106 μm

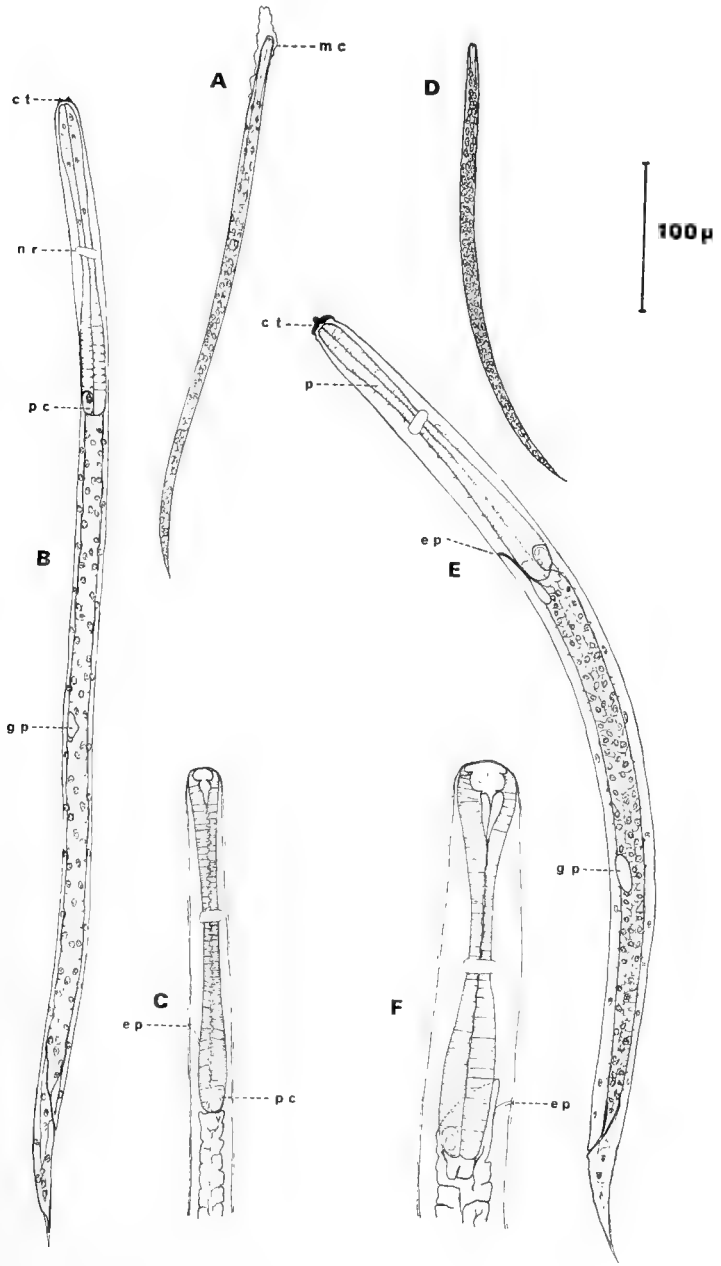
The fourth-stage larvae, or pre-adults, were described in detail by Janiszewska (1939) as the second larval stage from the intestinal wall. These larvae were found wandering through the gut-wall of the flounder feeding upon the tissues as they moved.

e. The immature adult (fig. 2):

Length :	600 (contracted) –2,100μm
Breadth :	113–332 μm
Oesophagus :	308–572 μm
Tail :	75–120 μm

These specimens were normally less than 2 mm. in length. It was not determined whether the final moult took place actually inside the body-wall or in the gut-lumen. The immature adults are similar in appearance to the mature adults, except that the sexual organs are not fully developed. The oral spines make their first appearance in the adult stage. These nematodes are capable of a great deal of contraction, and folds in the cuticle may form collars around the body. The behaviour of these immature adults is the same as that of the mature specimens.

FIG. 1. Cucullanid larvae. A. The second-stage larva of *Cucullanus heterochrous* within the first-stage larval cuticle. B. The third-stage larva of *C. heterochrous* from the flounder. C. The pre-adult of *C. heterochrous*. D. The first- or second-stage larva of *C. minutus*. E. The third-stage larva of *C. minutus* from the flounder. F. The pre-adult of *C. minutus*.
(ct, cuticular thickening; ep, excretory pore; gp, genital primordium; mc, moulted cuticle; nr, nerve ring; p, oesophagus; pc, large oesophageal cell)


A
mc
B
ct
nr
pc
gp
C
ep
pc
D
100μ
ct
p
E
ep
gp
F
ep

f. The mature adult:

Length :	2,000–3,800 μm
Breadth :	210–515 μm
Oesophagus :	430–580 μm
Tail :	70–160 μm

The mature adults have been described in detail by Gendre (1926), Törnquist (1931) and Berland (1970), and figured by MacKenzie & Gibson (1970). The females were generally longer and in most cases broader than the males. The adults live by moving freely amongst and feeding upon gut-contents, or, when food is not available, by attachment to and feeding upon the gut-wall of the flounder. Attachment to the gut-wall is brought about by the sucking action of the muscular oesophagus, by the collarette and associated oral spines situated on the lips and possibly by the spiny nature of the pseudobuccal cavity. Aspects of the behaviour of this species were discussed by MacKenzie & Gibson (1970).

(ii) Life-history.

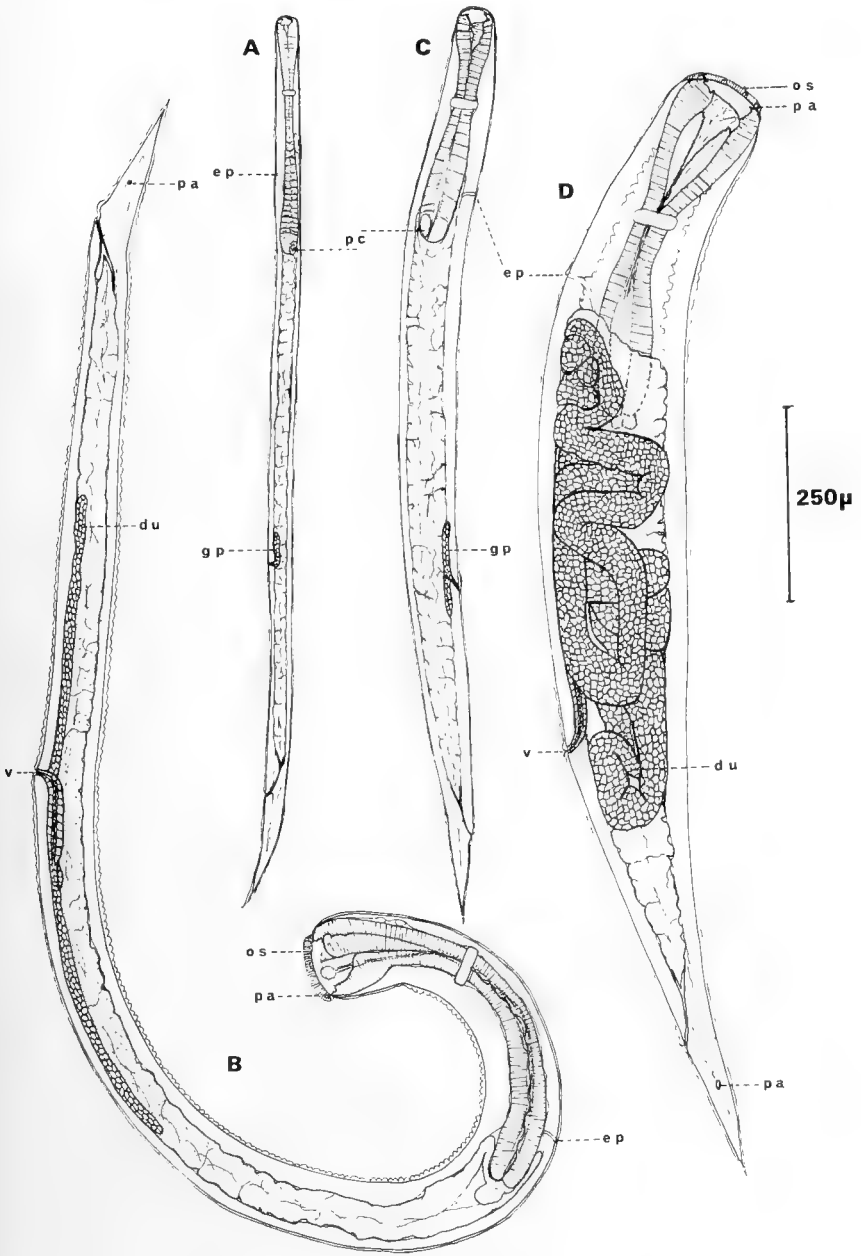
In flounders from the River Ythan third-stage larvae were present in small numbers throughout the year, but increased infestation occurred during the early spring (fig. 3), especially during March and April. Fourth-stage larvae were first found in March, but their numbers increased to a maximum during May and June and then fell to a very low level of infestation from August to November. Immature adults were first recovered in April, their numbers increased to a peak in June and July, and then their numbers fell in the autumn. Mature adults were first found in May, their numbers increased to a peak in July and August, and then fell off during the autumn with one or two individuals remaining until December.

In the marine flounders examined, the third-stage larvae were first recovered in January, the infestation had increased by March, but fell again by June (fig. 3). Fourth-stage larvae were first found in the March sample, the infestation was heavier in June, but had disappeared by September. Juvenile adults were recovered only from the June sample, and mature adults were found in the September and, to a greater extent, in the November samples.

(iii) Discussion.

The major period of egg-production of *C. minutus* in the River Ythan is during the summer months. This means that the eggs probably have time to embryonate and hatch during the late summer and autumn. This suggests that there is a gap of at least four to five months between the hatching of the eggs and the appearance of

FIG. 2. Cucullanid pre-adults and immature adults (all drawings are of female worms). A. Pre-adult *Cucullanus heterochrous*. B. Immature adult *C. heterochrous*. C. Pre-adult *C. minutus*. D. Immature adult *C. minutus*.
(ep, excretory pore; du, developing uterus; gp, genital primordium; os, oral spines; pa, papilla; pc, large oesophageal cell; v, vulva)


A
C
D
B
pa
ep
pc
du
gp
v
os
250μ

the third-stage larvae in the flounders. As in the case of *C. heterochrous* discussed below, there are a number of possible explanations for this apparent gap : (1) an intermediate host is involved, (2) small second-stage larvae were too small to be seen during the flounder examinations, (3) there is an earlier site of infestation where the second-stage larvae develop and moult into the third-stage larvae, and (4) the second-stage larvae develop and grow in the free-living state. With regard to the first possibility, Wülker (1930) suggested that decapods and cumaceans were involved as intermediate hosts, but Janiszewska's (1939) attempts to infest such crustaceans all failed. Markowski (1966) suggested that *Nereis diversicolor* Müller might serve as an intermediate host for *C. minutus*, and I too suspected this animal because it occurs in large numbers in muddy estuaries. However, my attempts to infest this species have all failed. Similarly, I have failed to infest or find cucullanid larvae in *Neomysis integer* (Leach), *Corophium volutator* (Pallas), gammarids and *Crangon vulgaris* L., though some development in the free-living state may be necessary before the larvae become infestive. One of the main arguments for the presence of an intermediate host is the accumulation of the majority of the larvae in the anterior intestinal wall of the flounder. The possibility that the second-stage larvae are present in the gut-wall but have not been seen is unlikely because both Janiszewska (1939) and myself have failed to detect them. The possibility that there is an earlier site of infestation in the flounder cannot be overlooked, though none were found by Janiszewska (1939) or by myself, since Le-Van-Hoa & Pham-Ngoc-Khue (1967) did find such a site when studying *C. chabaudi*. However, as suggested below, the appearance of the third-stage larvae occurs during the period when most of the large flounders are at sea on their spawning migration. Therefore, if the flounders are being infested by the parasite at that time, this accounts for the fact that *C. minutus* tends to infest the small flounders more heavily than the larger ones (unpublished information) and also accounts for the absence of these larvae in O-group flounders (those less than one-year old). If an earlier infestation of the flounders does occur then alternative explanations must be found for these two results. Evidence for the final possibility, i.e. that the larvae live for some months in the free-living state, is not very forthcoming either, except that free-living larvae are produced when the eggs hatch and that these can be kept alive for more than a week in 80% seawater. As in the case of *C. heterochrous* discussed below, it is not yet possible to favour any of these alternatives too strongly, though the first and the last possibilities do seem more likely. It is possible, therefore, that the first stage-larvae moult into the second-stage larvae, which is probably the infestive stage, and these grow, with or without the use of an intermediate host, and infest the flounder mainly in the winter and early spring.

Janiszewska (1939) stated that the infestation of the flounders with the third-stage larvae commenced in August, which is earlier than the major period of infestation recorded in flounders from the River Ythan. This difference might be explained by the fact that on the coast of Poland, where Janiszewska (1939) was working, the sea will be warmer in summer than the waters of the River Ythan, and therefore development will be faster. The fact that temperature does affect the development of *C. minutus* is discussed below. In warmer waters, therefore, it is

possible that infestation occurs in the autumn and mature specimens are found in the spring and summer, while in cooler waters the main period of infestation occurs in the early spring and mature adults are found in the late summer and autumn. In marine flounders from the Aberdeen area most of the mature adults were not found until the autumn, and this may account for the fact that third-stage larvae were not found in these fish in the autumn (fig. 3). The fact that the development of this parasite appears to take so long in marine flounders from the Aberdeen region may mean that in most cases the winter arrives and the parasite dies before egg production has really got underway. This could account for the small numbers of this parasite in these marine flounders.

B. *Cucullanus heterochrous*

The only previous comments on the life-history of this species were given by MacKenzie & Gibson (1970), and there is no previous record of the larval stages.

(i) Larval and adult development.

a. The egg:

Length : 75–102 μm
Breadth : 44–52 μm

The ova in the eggs cleaved in a similar manner to those of *C. minutus*, and larvae developed within the eggs after the same period of time. The eggs hatched after seven days at 19°C. and, like *C. minutus*, embryonation was not observed below 7°C.

b. The first-stage larva:

Length : 400–460 μm
Breadth : 12–14 μm

The first-stage larva developed within the egg, and after hatching was extremely active and capable of swimming. Any details of the anatomy of these larvae were difficult to see because of its small size and heavy concentration of nuclei. However, the anterior oesophagus could be distinguished in some specimens showing that it was very different from that of the adults because the musculature was much less developed.

c. The second-stage larva (fig. 1):

These larvae were so similar to the first stage-larvae that they could only be distinguished when parts of the moulted cuticle were still present. Such forms were found at 19°C. two days after hatching, though when the actual moult occurred is

not known: this may even have been inside the egg. The oesophagus could be seen more clearly in the second-stage larvae, and was about 165 μm in length. The remainder of the alimentary canal could not be seen, and there was no anus visible.

d. The third-stage larva (fig. 1):

Length :	660–955 μm
Breadth :	25–27 μm
Oesophagus :	240–293 μm
Tail :	78–93 μm

These larvae were found encysted in the gut-wall of the flounder within small round cysts. I have regarded this stage as the third-larval stage because (1) it is parasitic, (2) it is much larger than the second-stage larva, (3) there are morphological differences between the second-stage larva and this larva, and (4) nothing resembling a second-stage larva was ever recovered from the flounder. The oesophagus of these larvae was better developed than in the previous stages, and the large oesophageal cells were visible, as they were in the corresponding stage of *C. minutus*. In the lip-region cuticular thickenings, which may act like boring teeth, were visible. In female specimens (fig. 1) a genital primordium could be seen, though, unlike the equivalent stage of *C. minutus*, I could not ascertain the position of the excretory gland or the excretory pore. The intestine appeared to be in the form of a tube composed of a large number of cells, and for the first time a definite anus could be seen.

The third-stage larva of the closely-related *C. cirratus* Müller, 1777, was recently described by Berland (1970); but this description resembles the fourth-stage larva of *C. heterochrous*. Berland's argument for calling this larva the third-stage larva was because the development of the gonads resembles the third-stage larva of *Contracaecum aduncum* (Rudolphi, 1802), but there is no vulva present in *C. minutus* or *C. heterochrous* until the fourth larval stage. Therefore, because of this and the structure of the head, I consider Berland's specimens to be fourth-stage larvae.

e. The fourth-stage larva (figs 1 & 2):

Length :	620–1,600 μm
Breadth :	27–40 μm
Oesophagus :	240–359 μm
Tail :	89–133 μm

In these larvae, which were observed moulting from the third-stage larvae within the cysts in the gut-wall, the cuticular thickenings on the lips were lost and the oesophagus became similar in shape to that found in the adults. The fourth-stage larvae, or pre-adults, left the cysts and were recovered wandering through the tissues

of the gut-wall, feeding as they went. The lips possessed sharp edges which may have been associated with the movement through the tissues, because no oral spines or collarette were present at this stage. The large oesophageal cells were still visible, though they were not as clear as in the previous stage. In the female worms a developing uterus and vulva could be seen, though the vulva did not communicate with the exterior. The excretory pore was situated about half way between the nerve ring and the posterior edge of the oesophagus.

f. The immature adult (fig. 2):

Length :	1–6 mm.,	e.g. Length :	5,380 μm
		Breadth :	150 μm
		Oesophagus :	800 μm
		Tail :	173 μm

Oral spines and the collarette were present at this stage, and the pre-anal sucker and anal papillae were visible in males under a high powered microscope. In the females the uterus and ovaries were developing and the vulva could be seen to be connected to the exterior. These immature adults were found free in the lumen of the gut or attached to the gut-wall. It was not ascertained where in fact the final moult occurred or whether it was the pre-adults or the immature adults which migrated into the gut-lumen.

g. The mature adult:

Mature adults were described by Törnquist (1931) and Berland (1970). My specimens reached up to 12 mm., in the case of the females, and 10 mm. in length in the case of the males. These nematodes wandered through the intestinal contents of the flounder feeding as they went, though, like *C. minutus*, when food was not available they fed upon the gut-wall. Details of the migrations of these nematodes in the gut-environment have been given by MacKenzie & Gibson (1970).

In the past there has been some argument as to the nature of the structures which I have referred to as the oral spines. Gendre (1926), when discussing *C. minutus*, and Berland (1970) have commented that they may act as supporting 'ribs' for the cuticular collarette, and Berland (1970) also suggested that they may serve as an inter-locking device when the mouth is closed. My electron micrographs of *C. heterochrous* have shown that the spines, or denticulations, are, for at least the anterior-most part of their length, free of the collarette. They, therefore, probably aid the attachment of the parasite to the gut-wall, and may serve to split this wall and allow the muscular oesophagus to devour parts of the mucosa and sub-mucosa of the host.

(ii) Life-history:

The smallest larvae found in the flounders were the third-stage larvae. These were first recovered from the River Ythan in January, reaching a maximum in April, and then decreasing in numbers to zero in August, (Fig. 3). In marine flounders, however, these were found earlier, in November, when 8·8% of the fish examined contained small numbers of larvae. Due to the small size of these larvae small infestations may have been overlooked in the estuarine flounders, and this might account for this difference, but as mentioned below it is probable that there are no such larvae present in the Ythan estuary during these months. Fourth-stage larvae were first found in estuarine flounders during March. Their number increased to a maximum in May, and then decreased during the summer. In marine flounders their numbers increased during the late autumn and they were present in large numbers during the winter and spring. The dip in the level of infestation in marine flounders during the late winter may have been caused by the estuarine flounders entering the marine population at that time. Thus, as in the case of the third-stage larvae, the pre-adults are present in marine flounders long before they are in estuarine flounders.

Immature adults made their first appearance in the estuarine flounders during March, their numbers increased to a maximum intensity in June and a maximum incidence in July, and then their numbers decreased to zero by the following January. In marine flounders the numbers increased during the spring, as in Ythan flounders, but did not reach a peak until the autumn. This was possibly because the sea is cooler than the waters of the River Ythan during the summer months, and therefore development takes longer. These worms began to mature in estuarine flounders in September, mature adults increased in numbers to a maximum during the winter months and then decreased throughout the following spring. A similar effect was found in the marine flounders.

(iii) Discussion

The discrepancy in the periods of infestation with these larvae between the estuarine and the marine flounders could be the effect of temperature, since the waters of the River Ythan were warmer than the sea during the summer and cooler during the winter (H. D. Dooley, personal communication). However, there is a possibility that infestation with this parasite occurs much more frequently in the sea. This is suggested by the following facts: (1) infestation with this parasite is much heavier in marine flounders; (2) infestation with third-stage larvae proceeds earlier in marine flounders; and (3) this species tends to infest only the larger of the estuarine flounders (unpublished results) possibly because only the larger flounders participate in the spawning migration. It therefore appears that infestation of the marine flounders might occur before the arrival of the estuarine flounders in the sea, and the warmer temperature of the sea during the winter months probably allows faster development of these larvae in marine flounders. The sudden increase in the third-stage larval population in estuarine flounders in April is, therefore, probably associated with the return of some of the larger fish from the sea.

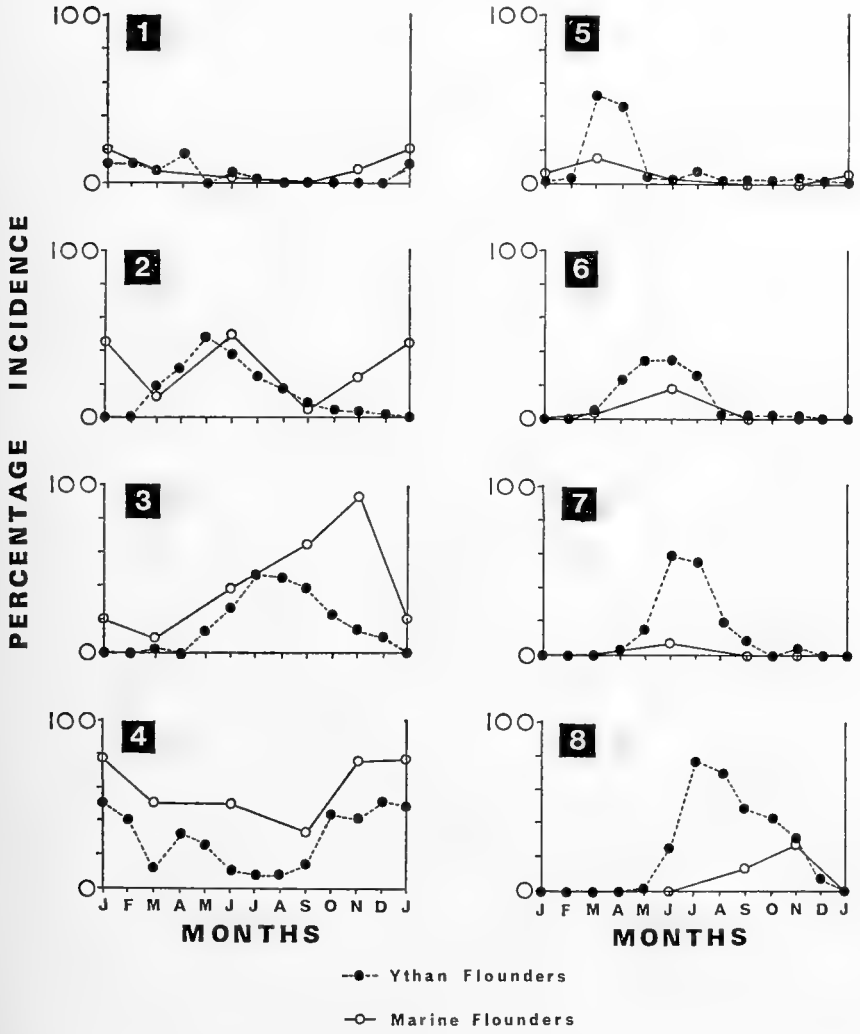


FIG. 3. The effect of season on the incidence of the larval and adult stages of *Cucullanus heterochrous* and *C. minutus* in flounders from the Ythan estuary and from the sea off Aberdeen. 1. The third-stage larvae of *C. heterochrous*. 2. Pre-adults of *C. heterochrous*. 3. Immature adults of *C. heterochrous*. 4. Mature adults of *C. heterochrous*. 5. Third-stage larvae of *C. minutus*. 6. Pre-adults of *C. minutus*. 7. Immature adults of *C. minutus*. 8. Mature adults of *C. minutus*.

The difference in size between the free-living second-stage larvae and the third-stage larvae recovered from the flounders suggests that: (1) smaller second- or third-stage larvae were missed during the examinations of the gut-wall; (2) there is an earlier site of infestation in the flounder; (3) there is an intermediate host; or (4) the second-stage larvae undergo a period of growth in the free-living state. Dealing with each point in turn, the first suggestion seems unlikely as no equivalent larvae were found by Janiszewska (1939) or myself in *C. minutus*. However, the second suggestion that there is an earlier site of infestation is a possibility, because Le-Van-Hoa & Pham-Ngoc-Khue (1967) found second-stage larvae of *C. chabaudi*, which migrated to the liver for the second moult, growing in the swim-bladder. It is therefore possible that such larvae might occupy a similar site in the body of the flounder. However, as stated below, it is most probable that most of the eggs hatch in the late spring and early summer, and therefore these larvae would be expected to infest the flounders at least by the autumn, long before the estuarine flounders enter the sea. Thus the high infestation in estuarine flounders returning to the estuaries in spring and the absence of larvae in O-group flounders cannot be explained by this suggestion, unless an earlier site of infestation is associated with the third and fourth suggestions. The third suggestion, that an intermediate host is involved, is doubtful because there is no evidence for the presence of such a host either in this species or in the other species of the genus discussed earlier. The life-cycle of the Camallanidae, nematodes with a similar mode of life, does in fact involve an intermediate host, but these are no longer thought to be closely related to the Cucullanidae (Inglis, 1967). The final suggestion, that the second-stage larvae grow in the free-living state, is suggested by the fact that free-living second-stage larvae were kept alive for more than a week in the laboratory. Both the third and the final suggestions would account for the apparent gap of several months between hatching and the appearance of the third-stage larvae in the flounders, the infestation acquired by the estuarine flounders when they entered the sea, and the absence of these larvae in O-group flounders. However, there is no further evidence for the latter suggestion, and, as stated by MacKenzie & Gibson (1970), the free-living larvae would penetrate neither the skin nor the gut-wall of the flounder. Though the larvae used for these latter experiments were recently hatched specimens, and it is possible that some development in the free-living stage is required before the larvae become infestive. It is clear that, at this stage, it is not yet possible to favour strongly any one of these suggestions until more information is available. Circumstances beyond my control hampered further work on this problem, but in my opinion the latter suggestion seems at present to be the most likely possibility, though the presence of an earlier site of infestation or possibility of an intermediate host cannot yet be overlooked.

In spite of the gap with regard to the actual method of infestation of the flounder, these results do give a good indication of what takes place during the life-history of this parasite. In my opinion, using the information given above, the life-history of *C. heterochrous* may occur as follows:

Most of the eggs are produced during the winter and early spring months, they hatch in the late spring and early summer when the water becomes warm enough

(7°C.) and release free-living first-stage larvae. These require a number of days to moult into the second-stage larvae, which live on the sea-floor, grow and become infestive in the late autumn, winter and following spring. This coincides with the appearance of the third-stage larvae in the flounders. Most of these larvae moult into fourth-stage larvae (pre-adults) around April to May (though perhaps much earlier in marine flounders), and from then until June to July they grow inside the gut-wall feeding upon the tissues. During these latter two months many of the pre-adults moult into small immature adults, which, in the lumen of the gut, proceed to grow and slowly mature until the late autumn, winter and early spring when they begin to produce eggs. The mature adults continue to grow and produce eggs until their numbers decline in the late spring and summer. Nearly all the old adults are lost by the autumn.

5. FINAL DISCUSSION

In both *C. minutus* and *C. heterochrous* in flounders from the River Ythan the main period of apparent infestation coincides with the spawning migration. The fact that larvae of *C. minutus* tended to infest the smaller flounders and those of *C. heterochrous* the larger flounders (unpublished information) might be explained thus: *C. minutus* is a very common parasite of flounders from the Ythan estuary (Gibson, 1972), and as the smaller flounders do not take part in the spawning migration they are much more available to the parasite at this time, and, similarly, *C. heterochrous* is a very common parasite of flounders from the sea off Aberdeen (Gibson, 1972) and, as it is only the larger flounders which migrate into the sea, they will stand a better chance of becoming infested. It therefore appears that large flounders may migrate into the sea and become infested with *C. heterochrous* while the small flounders remain in the estuary and become more heavily infested with *C. minutus*.

In marine flounders *C. minutus* does not appear to develop to maturity until several months later than it does in estuarine flounders. This may be caused by the fact that the water-temperature of the Ythan estuary is warmer than that of the sea during the summer. The possibility that the development of this parasite is affected by temperature is also suggested by the fact that mature specimens were obtained from flounders at Plymouth in April, two months earlier than in flounders from the Ythan estuary. Further evidence can be deduced from the work of Markowski (1966), who found *C. minutus* in flounders from a brackish water reservoir containing water partially heated by the cooling water of a power-station, and in the sea a few yards away only a small number of flounders were infested with this parasite. When the zoogeography of this species is studied it is noticeable that *C. minutus* has not been found in northern waters except by Rudolphi (1819) and Janiszewska (1939) in the Baltic Sea. von Linstow (1904) reported *Dacnitis fusiformis* Molin, a synonym of *C. minutus*, from the Murman coast; but his specimens were from the rectum of the flounder and, as shown by MacKenzie & Gibson (1970), *C. minutus* is very rarely found in the rectum of the flounder, whereas *C. heterochrous* is most commonly found in that region of the gut. *C. minutus* has normally been found in a more southerly geographical area, e.g. Gendre (1926) in French estuaries,

Stossich (1890, 1898) and Mola (1928) in the Mediterranean Sea, and Butzkaya (1952), Radulescu & Vasiliu-Suceveanu (1956), Bykhovskaya-Pavlovskaya et al. (1964), Komarova (1966), Markevitch (1967) and Naidenova (1970) in the Black Sea and its associated estuaries. On the other hand *C. heterochrous*, 'the winter species', has been recorded mainly in the North Sea, the Russian Arctic, the Siberian coast and the Gulf of the St. Lawrence, e.g. Nicoll (1907), Baylis (1928), Wülker (1930), Schuurmans Stekhoven (1935), Kreis (1952), Polyanski (1955), Zhukov (1960), Strelkov (1960), Berland (1961, 1970) and Ronald (1963). This species has been recorded further south only on a small number of occasions, e.g. Stossich (1892, 1898),* as *Dacnitis foveolatus* (Rud.), in the Mediterranean Sea and Gendre (1927) off the north-west coast of Africa. It therefore appears that *C. minutus* is a parasite of flatfish living in warmer water than *C. heterochrous*, and that Aberdeen is close to the northern limit of *C. minutus* in a marine environment and is in a position where the ranges of these two parasites overlap. Further north it is probable that, except in estuarine conditions which are warmer than the sea during the summer, *C. minutus* would not be capable of completing its full life-cycle in one year. The Baltic Sea may be an exception to this, as its isolation from the Atlantic Ocean and shallowness means that it is warmer in summer than equivalent latitudes of the North Sea, and, with its lower salinity, it is therefore suitable for the development of this parasite. The slow development and relatively long life of *C. heterochrous* contrasts with the fast development and short life of *C. minutus*, for if the above interpretations of the results are correct, the life-history of *C. heterochrous* takes two years for completion and that of *C. minutus* only one year. This may explain the fact that *C. heterochrous* is able to occupy a more northerly geographical range than *C. minutus*.

6. ACKNOWLEDGEMENTS

I should like to thank Dr. H. H. Williams for his advice and encouragement during the course of this work. I also wish to thank Professor V. C. Wynne-Edwards for the use of the facilities of his department at the University of Aberdeen where most of this work was carried out and the Scientific Research Council for a grant. I am grateful to Dr. J. P. Harding and Mr. S. Prudhoe for reading the manuscript.

7. REFERENCES

Baylis, H. A. 1928. Records of some parasitic worms from British vertebrates. *Ann. Mag nat. Hist.* (10) **1** : 329–343.

Berland, B. 1961. Nematodes from some Norwegian fishes. *Sarsia* **2** : 1–50.

—— 1970. On the morphology of the head in four species of the Cucullanidae. *Sarsia* **43** : 15–64.

Butzkaya, N. A. 1952. Parasitic fauna of the Black Sea economic fishes in the pre-estuarine area of the Danube. *Trud. Leningr. Soc. Nat.* **71** (4) : 30–52 (In Russian).

Bykhovskaya-Pavlovskaya, I. E. et al. 1964. *Key to the parasites of freshwater fish of the U.S.S.R.* Israel Program for Scientific Translation, Jerusalem.

* Stossich's specimens were not from flatfish and may therefore not have been *C. heterochrous*.

GENDRE, E. 1926. Sur un nématode peu connu, *Cucullanus fusiformis* Molin. *P.-v. Soc. linn. Bordeaux* **78** : 39–49.

—— 1927. Parasitologia Mauritanica. Helmintha (2): Nématodes parasites des poissons de la côté de Mauritanie (Suite). *Bull. Com. Étud. hist. scient. Afr. occid. fr.*, N.S. **21** : 1–14.

GIBSON, D. I. 1972. Flounder parasites as biological tags. *J. Fish Biol.* **4** (1) : (In Press).

INGLIS, W. G. 1967. The relationships of the nematode superfamily Seuratoidea. *J. Helminth.* **41** : 115–136.

JANISZEWSKA, J. 1939. Studien über die Entwicklung und die Lebenweise der parasitischen Würmer in der Flunder (*Pleuronectes flesus* L.). *Mém. Acad. pol. Sci.*, ser. B, **14**, 1–68.

KOMAROVA, T. I. 1966. Helminth fauna of edible fish of the Dnieper estuary. In: Mazurmovich (edit.). Parasites, intermediate hosts and vectors. *Akad. Nauk Ukr. SSR. Kiev, ser. Problemy Parasit.* **6** : 57–66 (In Russian).

KREIS, H. A. 1952. Beiträge zur Kenntnis parasitischer Nematoden. 10. Parasitische Nematoder aus der Umgebung der Färöer. *Vidensk. Meddr dansk naturh. Foren.* **114** : 251–307.

LE-VAN-HOA & PHAM-NGOC-KHUE. 1967. Morphologie et cycle évolutif de *Cucullanus chabaudi* n. sp., parasites des poissons, *Pangasius pangasius* H.B. (*P. buchanani*) du Sud Viet-Nam. *Bull. Soc. Path. exot.* **60** : 315–318.

LINSTOW, O F. B. VON. 1904. Entozoa des zoologischen Museums der Kaiserl-Akademie der Wissenschaften zu St. Petersburg. II. *Ezheg. zool. Muz.* **8** : 265–294.

MACKENZIE, K. & GIBSON, D. I. 1970. Ecological studies of some parasites of plaice *Pleuronectes platessa* L and flounder *Platichthys flesus* (L.). *Symp. Br. Soc. Parasit.* **8** : 1–42.

MARKEVITCH, A. P. 1967. Analysis of parasitic fauna of Ukrainian fish from ecological and geographical respects. *Proc. Zool. Soc. U.A.R.* **2** : 169–179.

MARKOWSKI, S. 1966. The diet and infection of fishes in Cavendish Dock, Barrow-in-Furness. *J. zool. Lond.* **150** : 183–197.

MOLA, P. 1928. Vermi parassiti dell'ittiofauna italiana. Contributo alla patologia ittica. *Boll. Pesca. Piscic. Idriobiol.* **4** : 395–443.

NAIDENOVA. N. N. 1970. The parasite fauna of fish in the family Gobiidae from the Azov Sea. In: Delyamure (edit.). Parasites of marine molluscs, fish and mammals. *Akad. Nauk. Ukr. SSR. Biologiya Morya. Kiev.* **20** : 74–84 (In Russian).

NICOLL, W. 1907. A contribution towards a knowledge of the entozoa of British marine fishes. Part I. *Ann. Mag. nat. Hist.* (7) **19** : 66–94.

POLYANSKI, Y. I. 1955. Parasites of the fish of the Barents Sea. *Trudy zool. Inst., Leningr.* **19** : 5–170 (In Russian). (Translation: Israel Program for Scientific Translation, Jerusalem, 1966).

RADULESCU, I. & VASILIU-SUCEVEANU, N. 1956. Contributiuni la cunoasterea parazitilor pestilor din complexul lagunar Razelm-Sinoe. *Anal. Inst. cerc. pisc.* **1** : 309–333 (In Roumanian, French & Russian).

RONALD, K. 1963. The metazoan parasites of the Heterosomata of the Gulf of the St. Lawrence. VII. Nematoda and Acanthocephala. *Can. J. Zool.* **41** : 15–21.

RUDOLPHI, C. A. 1819. *Entozoorum synopsis cui accedunt mantissa duplex et indices locupletissimi.* Berolini.

SCHUURMANS STEKHOVEN, J. H. 1935. Nematoda parasitica. *Tierwelt N.-u. Ostee.* Tiel 5. c. **28** : 1–50.

SHULMAN, S. S. 1957. Material on the parasitofauna of lampreys from the basins of the Baltic and White Seas. *Bull. All-Union Sci. Res. Inst. Lake and River Fisheries* **42** (In Russian). (Translation in: *Parasites and diseases of fish.* Edit., Petrushevskii, G. K. Israel Program for Scientific Translation, Jerusalem, 1966.)

STOSSICH, M. 1890. Brani di elmintologia tergestina. *Boll. Soc. adriat. Sci. nat.* **12** : 39–47.

—— 1892. Osservazioni elmintologiche. *Glasn. hrv. narodsl. Drust.* **7** : 64–73.

—— 1898. Saggio di una fauna elmintologica di Trieste e provincie contermini. *Prog. Civ. Scuola R. Sup., Trieste*, 1–162.

STRELKOV, J. A. 1960. Endoparasitic worms of marine fishes of east Kamchatka. *Trudy zool. Inst., Leningr.* **28** : 146–196 (In Russian).

TÖRNQUIST, N. 1931. Die Nematodenfamilien Cucullanidae und Camallanidae, nebst weiteren Beiträgen zur Kenntnis der Anatomie und Histologie der Nematoden. *Göteborgs K. Vetensk.-o. VitterhSamh. Handl.* 5f, s.B, **2** : 1–441.

VESSICHELLI, N. 1910. Di un nuovo *Dacnitis* parasitta del *Petromyzon planeri* *Monitore zool. ital.* **21** : 304–307.

WÜLKER, G. 1930. Über Nematoden aus Nordseetieren I. *Zool. Anz.* **87** : 293–302.

ZHUKOV, E. V. 1960. Endoparasitic worms of fishes from the Sea of Japan and South Kuril shallow-waters. *Trudy zool. Inst., Leningr.* **28** : 3–146 (In Russian).

Dr D. I. GIBSON
Department of Zoology
BRITISH MUSEUM (NATURAL HISTORY)
CROMWELL ROAD
LONDON SW7 5BD

A LIST OF SUPPLEMENTS TO THE ZOOLOGICAL SERIES OF THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY)

1. KAY, E. ALISON. Marine Molluscs in the Cuming Collection British Museum (Natural History) described by William Harper Pease. Pp. 96; 14 Plates. 1965. (Out of Print.) £3.75.
2. WHITEHEAD, P. J. P. The Clupeoid Fishes described by Lacepede, Cuvier and Valenciennes. Pp. 180; 11 Plates, 15 Text-figures. 1967. £4.
3. TAYLOR, J. D., KENNEDY, W. J. & HALL, A. The Shell Structure of Mineralogy at the Bivalvia. Introduction. Nuculacea-Trigonacea. Pp. 125; 29 Plates, 77 Text-figures. 1969. £4.50.
4. HAYNES, J. R. Cardigan Bay recent Foraminifera (Cruises of the R.V. *Antur*) 1962–1964. (*In press.*)

Printed in England by Staples Printers Limited at their Kettering, Northants establishment

BATS FROM THAILAND AND CAMBODIA

J. E. HILL
AND
KITTI THONGLONGYA

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 22 No. 6
LONDON: 1972

BATS FROM THAILAND AND CAMBODIA

BY
JOHN EDWARDS HILL
AND
KITTI THONGLONGYA

Pp. 171–196; 4 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 22 No. 6
LONDON: 1972

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 22, *No.* 6 *of the Zoological series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation
Bull. Br. Mus. nat. Hist. (Zool.).

© Trustees of the British Museum (Natural History), 1972

TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 29 *March*, 1972 *Price* 95p

BATS FROM THAILAND AND CAMBODIA

By J. E. HILL & KITTI THONGLONGYA

INTRODUCTION

THE chiropteran fauna of southeast Asia as a whole is as yet not fully understood and knowledge of the bats of Thailand and Cambodia in particular rests largely on the efforts of a limited number of collectors. In recent years a more active interest in the bats of the region has become apparent and as a result a number of specimens have been received for determination at the British Museum (Natural History). Some of these have led towards the solution of taxonomic problems of long standing: others represent new records or range extensions for Thailand and Cambodia or are examples of taxa rare in collections. The majority of the specimens originate from Thailand and have been obtained over several years by Dr. J. T. Marshall of the United States Army Medical Component, South East Asia Treaty Organization. These were examined initially in Thailand by the junior author and are now in the collection of the British Museum (Natural History), except for a number of duplicate specimens sent to the Smithsonian Institution, Washington. A few specimens collected by the junior author are from the Thai National Reference Collection of which he is Curator. Cambodian specimens obtained by Mr. J. M. Klein are from the Museum National d'Histoire Naturelle, Paris, a small series of duplicates being retained in the British Museum (Natural History). Measurements are in millimetres: the minimum, maximum and mean (in parentheses) are given for series.

ACCOUNT OF SPECIES

Rousettus amplexicaudatus amplexicaudatus (E. Geoffroy, 1810)

THAILAND: Doi Pha Hom Pok, Fang, Chiangmai, 6,800 feet, c.18° 47′ N., 98° 59′ E. 1 ♂ (young).

Phu Nam Tok Tap Kwang, Kaeng Khoi, Sara Buri, c. 14° 42′ N., 100° 52′ E. 2 ♂♂ (1 young).

The specimen from Doi Pha Hom Pok confirms the record by Chasen (1940 : 29) of *R.a. amplexicaudatus* from the mountains of northern Thailand, a region apparently on the northwestern border of its distribution.

Rousettus leschenaulti leschenaulti (Desmarest, 1820)

THAILAND: Koh Klet, Pak Klet, Nonburi, 13° 50′ N., 100° 29′ E. 1 ♂.

Bang Phra, Siracha, Chonburi, 13° 12′ N., 100° 57′ E. 8 ♂♂ (6 young), 6 ♀♀ (young).

Recorded hitherto from the mountainous northern part of Thailand by Chasen (1940: 29). Specimens (B.M. 14.12.8.31–34) reported from Tagoot, Tenasserim, Burma as *R. leschenaulti* by Wroughton (1915: 702) are in fact *R. amplexicaudatus*.

Pteropus hypomelanus Temminck, 1853

THAILAND: Tao Poon, Koh Som, Koh Samui, Surat Thani. 1 ♂ (young), 2 ♀♀ (1 young).

The small islet of Koh Som is close by the larger island of Samui, in the Bight of Bandon off the east coast of southern Thailand. No collector of mammals appears to have visited it hitherto although Koh Samui was visited by H. C. Robinson and C. B. Kloss in 1913 on behalf of the Federated Malay States Museum. No *Pteropus* were encountered (Robinson and Kloss, 1915a) and the genus was first reported from the islands by Marshall and Vandee (1970 : 504) who recorded these and other specimens obtained in 1968. *Pteropus hypomelanus* is known to occur on a number of the other small islands off the east coast of the Malay Peninsula and on the Natuna Islands.

The back of the adult female from Koh Som is black, streaked with grey, the mantle bright chestnut and the head greyish, tinged with buff. The underparts are predominantly grey brown or hair brown, excepting for a band of black across the base of the throat. The young male and female have less grey on the back, the mantle bright chestnut in the male and deep rufous in the female, both with blackish brown crown and nape and with black underparts. Measurements of the adult female: length of forearm 141; greatest length of skull 64·3; condylobasal length 62·3; palatal length 36·9; least interorbital width 8·4; postorbital width 7·6; zygomatic width 31·6; braincase width 21·6; mastoid width 19·9; c^1–c^1 11·0; m^1–m^1 17·6; c–m^2 24·3; length of mandible 48·9; c–m_3 27·4.

It is difficult to refer these specimens to any of the subspecies of *P. hypomelanus* so far described from the islands of the South China Sea. The darker back and greyish or black brown crown and nape set them apart from the pale subspecies *P.h. lepidus* from the majority of the east coast islands of the Malay Peninsula and *P.h. canus* and *P.h. annectens* from the North and South Natuna Islands: although the colour of the back resembles that of *P.h. condorensis* from Con Son Island (Pulo Condore), in this subspecies the crown and nape are chestnut brown like the mantle. Andersen (in Kloss, 1916 : 38) reports specimens of *P.h. condorensis* from certain of the small islands off the southeastern coast of Thailand. These are not in the collection of the British Museum (Natural History) and although the same size as the adult from Koh Som, from the description some examples differ from the Koh Som specimens in the colour of the underparts. Unfortunately, Andersen did not mention the colour of the crown and nape. Insufficient material is available to demonstrate the extent of colour variation in *condorensis*, and for the present specimens from Koh Som are left unallocated to subspecies.

They are very similar in colour and size to *P.h. geminorum*, so far known from the islands of the west coast of the Peninsula from Paya, off Kedah, States of Malaya, north to the Mergui Archipelago, whence there are specimens in the British Museum (Natural History) from the islands of Barwell, Sir John Hayes, Malcolm and the Gregory group. The adult female from Koh Som corresponds to the hair brown phase of *geminorum* noted by Andersen (1912 : 107): the bright chestnut mantle contrasts with the dark seal brown mantle usual in this phase of *geminorum*, but a

similar condition is exhibited by a specimen from Sir John Hayes Island. The two younger specimens correspond to the black-bellied phase noted by Andersen (p. 106). *Pteropus hypomelanus* is found predominantly on islands and has yet to be recorded from the mainland of the Malay Peninsula. It is of interest therefore to report the occurrence of similar populations on small islands lying off the eastern and western coasts at approximately the same latitude.

Cynopterus sphinx angulatus Miller, 1908

THAILAND: Doi Pha Hom Pok, Fang, Chiangmai, 6,800 feet, c. 18° 47′ N., 98° 59′ E. 1 ♂, 2 ♀♀.

Doi Ithanon, Chom Thong, Chiangmai, 1,700 metres. 18° 35′ N., 98° 29′ E. 1 ♂.

Phu Nam Tok Tap Kwang, Kaeng Khoi, Sara Buri, c. 14° 21′ N., 100° 52′ E. 1 ♀.

Bang Phra, Siracha, Chonburi, 13° 12′ N., 100° 57′ E. 22 ♂♂ (3 young), 25 ♀♀.

Koh Klet, Pak Klet, Nonburi, 11 miles north of Bangkok. 1 ♂, 1 ♀.

Lumpinee, Bangkok. 1 ♂, 1 ♀.

CAMBODIA: Prek Tasek, 8 kilometres northwest of Phnom Penh. 1 ♀. Siem Reap. 1 ♀.

In his monographic study of the Megachiroptera, Andersen (1912) recognized a single species of *Cynopterus*, *C. brachyotis*, in the Malay Peninsula, with two sympatric subspecies, one, *C.b. brachyotis*, with shorter ears and rostrum, the other, *C.b. angulatus*, having longer ears and rostrum. According to Andersen, both occur in Sumatra and throughout much of the Peninsula but *C.b. angalatus* alone extends north of the Peninsula as far as northern Thailand. Neither was thought by Andersen to have any close affinity to the Indian and Javan species *C. sphinx* which he thought occurred on the mainland as far east as northern Thailand (where according to Andersen it is to be found sympatrically with *C.b. angulatus*), although a subspecies, *C.b. titthaecheilus*, was recognized by this author in Java.

However, Kloss (1911 : 185) listed *angulatus* as a distinct species, noting an affinity to *C. sphinx* and suggesting that *angulatus* should be regarded as the southern race of the Indian species. Later, Robinson and Kloss (1915a : 133, 1915b : 114) reiterated this suggestion as a logical conclusion, although in both instances these authors follow Andersen in listing *angulatus* as a subspecies of *brachyotis*. This led to an exchange of opinion by Andersen and Kloss (1915 : 220) in which the views of Andersen seem rather doubtfully to prevail. His opinion is published again in Kloss (1916 : 40), who provides further (p. 41) comments on specimens from the islands off southeastern Thailand among which Andersen had identified both *C.b. brachyotis* and *C.b. angulatus*. Kloss clearly remained unconvinced and later (1917 : 300; Robinson and Kloss, 1918 : 26; Kloss, 1919 : 361) reverted to the view that *angulatus* represented a distinct species. Subsequently, Chasen (1940 : 25) considered *angulatus* to be a large subspecies of *brachyotis* occurring only in the north of the Malay Peninsula and in some nearby islands, a view adopted by Hill (1961 : 630) and Medway (1969 : 12).

It is evident from the literature that specimens from southern Thailand are critical to any study of the status of *angulatus*. Sanborn (1952 : 2) for example

referred specimens from Kwan Don Setul (=Satun) Province to this form but pointed out that some of the specimens examined had ears and rostra which agreed with *C. sphinx*. In fact, this series reported by Sanborn from a locality almost on the border with Malaya has measurements (length of forearm 61·0–72·4, of ear 16·5–22·0) indicating that it includes both *angulatus* and *brachyotis*. These appear to occur together in Perak, in the northern States of Malaya (Andersen, 1912 : 614; Hill, 1961 : 630); on Koh Lak, off the northeastern part of the Malay Peninsula in southern Thailand (Gyldenstolpe, 1916 : 9); on the islands off southeastern Thailand (Andersen, in Kloss, 1916 : 40); and now, in the present collection, at Bang Phra, Siracha, yet further north.

Furthermore, specimens of *brachyotis* have been obtained at Khao Luang, Nakhon Si Thamrat, on the eastern side of the Peninsula, which is north of Trang, the type locality of *angulatus*, on the opposite side of the Peninsula. More material than was available to Andersen now exists in the collection of the British Museum (Natural History): in particular, there are good series of specimens from central Burma, from Tenasserim (Wroughton, 1915 : 703) and the Mergui Archipelago (Lindsay, 1927 : 44), from central and northern Thailand, and from the Malay Peninsula (Hill, 1961 : 630).

The specimens now available from this critical area divide into two groups, one of larger examples with longer forearms and ears, the other group with generally shorter forearms and shorter ears (the length of the ear as given here is from the meatus, measured personally or for dry specimens by the collector). These correspond to *angulatus* and *brachyotis* as these are defined by Andersen (1912). It is difficult to postulate so extensive an area of intergradation in order to maintain the opinion that *angulatus* and *brachyotis* are conspecific. There are two alternatives to the view that *angulatus* is a subspecies of *brachyotis*, namely that it is a species distinct from either *brachyotis* or from *sphinx*; or that it is a subspecies of *sphinx*. The latter alternative is adopted here and is supported by the long series of specimens from Burma and Thailand which show that the criterion of rostral length used by Andersen to separate *angulatus* and *C. sphinx sphinx* is by no means as exclusive as was thought by that author.

Andersen (pp. 600, 612) considered that *angulatus* might be distinguished from *C.s. sphinx* by a shorter rostrum, its length in *angulatus* being less than one quarter of the total length of the skull, in *sphinx* one quarter or more. The rostral lengths of specimens from India (*C.s. sphinx*, *C.s. gangeticus*), Burma (*C.s. sphinx*), Thailand, Malaya and Sumatra (*angulatus*) and Java (*C.s. titthaecheilus*) are compared graphically against total skull length in Figure 1, the dotted line demonstrating those points at which the rostral length is one quarter of the total skull length. There is no clear separation between Indian, Burmese and Thai specimens and, indeed, in *sphinx* from Ceylon and *titthaecheilus* from Java the length of the rostrum is not infrequently less than one quarter of the total length of the skull. The specimens obtained by Dr. Marshall in Thailand are very slightly smaller than *C.s. sphinx* and have relatively slightly shorter rostra, in these features resembling specimens from Tenasserim and the Malay Archipelago.

There appears to be no exclusive external or cranial feature by which *C. sphinx*

can be separated from *C. brachyotis*, a difficulty recognized by Andersen (1912 : 609) who noted that the numerous subspecies of *C. brachyotis* taken together could be separated from the modifications of *C. sphinx* only by their relatively shorter ears. *Cynopterus sphinx* is distributed from India and Ceylon through Burma, Thailand and Indochina to Hong Kong: it extends in the Malay Peninsula as far south as Perak and thence to Sumatra, Java and Timor. Occurring more frequently on islands, *C. brachyotis* extends from Borneo and the Philippine Islands to Java, Sumatra, the Malay Peninsula and its adjacent islands northwards at least as far as southern Thailand and North Vietnam (*C.b. hoffeti* Bourret, 1944), occurring also on the Nicobar Islands and Ceylon. Although on occasion some subspecies (*C.b. scherzeri* from the Nicobar Islands, *C.b. insularum* from Kangean and Mata Siri Islands, off Java) approach or equal the smaller of *C. sphinx* in size, such subspecies have the characteristically smaller ears of *brachyotis*.

There is some overlap between the two species in the area of sympatry from Thailand to Sumatra in both length of forearm and ear, and although a definitive line cannot be drawn for either character, the majority of specimens can be separated readily by a combination of these parameters, which are compared for Burma, Tenasserim, Thailand and Indochina in Figure 2 and for Malaya and Sumatra in Figure 3. A comparable comparison of specimens of *sphinx* and *brachyotis* from Ceylon and Java appears in Figure 4. On the mainland and in Sumatra, the

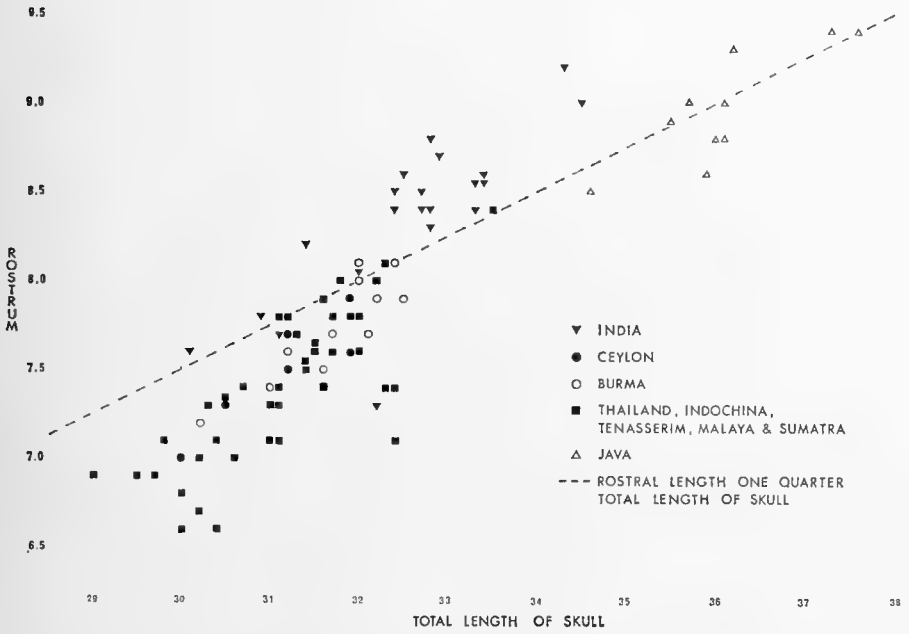


FIG. 1. Length of skull and rostrum (front of orbit to nares) in *Cynopterus sphinx*.

forearm length of specimens referable to *sphinx* generally exceeds 65 mm. and the length of the ear is greater than 19·0 mm., while specimens referable to *brachyotis* have forearm and ear lengths only rarely exceeding these values.

The large number of specimens from Thailand show that *C.s. angulatus* has ears that in length considerably exceed the maximum value of 18·0 mm. which Andersen (1912 : 612) noted for *angulatus* when he allocated it to *brachyotis* as a subspecies. In this connection it should be noted that Andersen stated (p. 612) of *angulatus* that the measurement of the ear is from the orifice, yet in the typical series measured by Miller (1898 : 318) the length of the ear from the meatus is given as 18–21 mm. and from the crown 15–18 mm., only the latter being under the maximum given by Andersen for *angulatus*. Still further, the table of measurements in a British Museum (Natural History) copy of Miller (1898) has been annotated (p. 318) by Andersen to the effect that he has examined the first six specimens tabulated. The

FIG. 2. Length of forearm and ear in *Cynopterus sphinx* and *C. brachyotis*.

first of these (U.S. National Museum 83,524) with forearm of 61 mm. and ear 18·4 mm. he notes as *C.s.* (sic) *brachyotis*, the remainder as true *angulatus*, thus demonstrating that the two forms occur together at the type locality of *angulatus*, Trang, in southern Thailand.

The montane subspecies *C. brachyotis altitudinis* Hill, 1961, from Mount Brinchang, Perak has generally longer ears than *C.b. brachyotis*, reaching a maximum of 20 mm., but has a short forearm only exceptionally reaching a maximum length of 67 mm. Furthermore, it is linked to *C.b. brachyotis* from the surrounding lowlands by intermediates (Hill, 1961 : 632).

Chasen (1940 : 25) listed the large *C. major* Miller, 1902, from Nias Island, off west Sumatra as a subspecies of *sphinx*. Andersen (1912 : 630) considered it a representative of '*C. brachyotis angulatus*' on account of its ears which he noted (p. 629) as 16·5–18 mm. in length, but Chasen (p. 29) measured the length of the ear at 18·5–20 mm.

Cynopterus brachyotis brachyotis (Müller, 1838)

THAILAND: Khao Luang, Nakhon Si Thamrat, 1,300 feet, 8° 26′ N., 99° 58′ E. 3 ♂♂ (1 young), 1 ♀.

Bang Phra, Siracha, Chonburi, 13° 12′ N., 160° 57′ E. 1 ♂, 5 ♀♀.

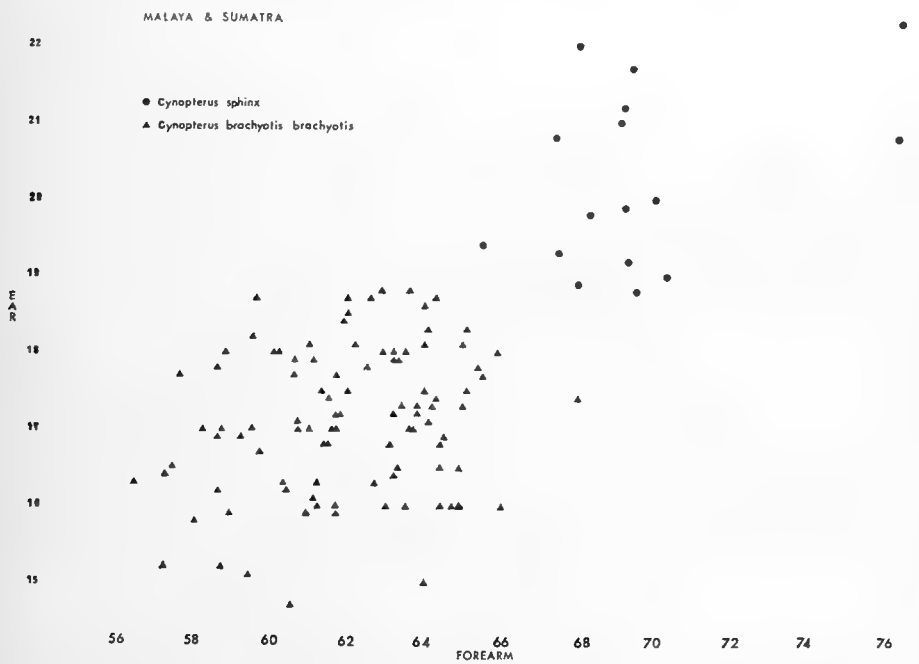


FIG. 3. Length of forearm and ear in *Cynopterus sphinx* and *C. brachyotis*.

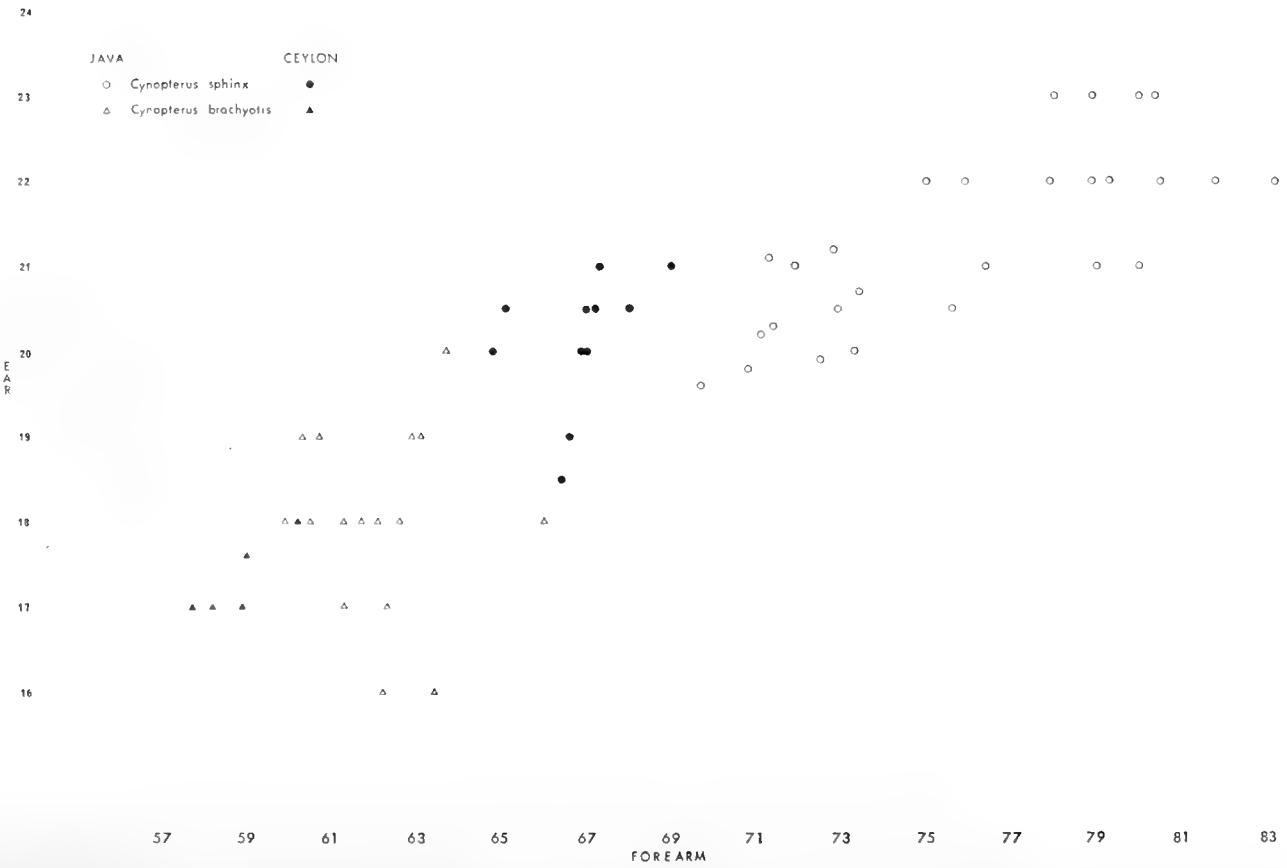


FIG. 4. Length of forearm and ear in *Cynopterus sphinx* and *C. brachyotis*.

These specimens agree exactly with *C.b. brachyotis* from the southern part of the Malay Peninsula: those from Bang Phra constitute the northernmost record in Thailand: *C.b. brachyotis* occurs also on the islands of Chang, Mehsi East, Kra, Klum, Kut and Lak in the Gulf of Siam.

Megaerops ecaudatus (Temminck, 1837)

THAILAND: Khao Luang, Nakhon Si Thamrat, 1,300 feet, 8° 26′ N., 99° 58′ E. 1 ♂, 1 ♂.

Doi Pha Hom Pok, Fang, Chiangmai, 6,800 feet, 18° 47′ N., 98° 59′ E. 1 ♂.

This species apparently has not been recorded hitherto from Thailand although known from Malaya (Bonhote, 1903 : 15; Hill, 1961 : 636) and both North and South Vietnam (Van Peenen, Ryan and Light, 1969 : 41).

Chironax melanocephalus (Temminck, 1825)

THAILAND: Khao Luang, Nakhon Si Thamrat, 1,300 feet, 8° 26′ N., 99° 58′ E. 1 ♀.

No skull is available to confirm the identification of this specimen as *C. melanocephalus*, but it has the characteristically darker head of that species with bright orange patches at the sides of the throat just anterior to the shoulders. *Chironax melanocephalus* has been reported from Selangor (Chasen, 1940 : 30, Hill, 1961 : 640) and, more recently, specimens (B.M.67. 1484–1488) have been received from Gunong Benom, Pahang, but the species has not before been reported from Thailand. The specimen from Khao Luang agrees well with one from Pahang but the head is a little less intensely black, the underside rather more brownish and the orange throat patches less prominent. Length of forearm 47·3.

Sphaerias blanfordi (Thomas, 1891)

THAILAND: Doi Pha Hom Pok, Fang, Chiangmai, 6,800 feet, 18° 47′ N., 98° 59′ E. 1 ♀ (young adult).

This species has evidently an extensive range through the montane areas of southeastern Asia. The original material consisted of three examples (one, B.M.90.4.7.6, in the collections of the British Museum (Natural History)) collected by Fea at Leito, Cheba, Karin Hills, Burma at 1,000 metres, while subsequently Allen and Coolidge (1941 : 136) recorded two specimens from Mount Angka (Doi Inthanon), in northern Thailand, at 4,000 feet. More recently, Bhat (1968 : 471) has recorded *S. blanfordi* from various Indian localities in Uttar Pradesh, at elevations ranging from 800 to 2,710 metres. Measurements of the specimen from Doi Pha Hom Pok: length of forearm 52·0; total length of skull 27·8; condylobasal length — ; condylocanine length – ; length orbit to nares 7·0; lachrymal width 7·0; least interorbital width 5·3; postorbital width 6·7; zygomatic width 15·5; diameter of orbit 6·5; braincase width 11·8; mastoid width 11·3; c^1–c^1 5·8; least width between bases of canines 3·1, p^4–p^4 5·3, least width between p^4–p^4 4·7; m^1–m^1 7·5; least width between m^1–m^1 5·6; width mesopterygoid fossa 3·8; c–m^1 8·6; length of mandible 19·9; coronoid height 7·7; c–m_2 9·8.

Macroglossus minimus sobrinus Andersen, 1911

THAILAND: Doi Inthanon, Chom Thong, Chiangmai, 1,700 metres, 18° 35′ N., 98° 29′ E. 1 ♀.

Ban Bangmakham, Koh Samui, Surat Thani, 9° 30′ N., 100° 00′ E. 1 ♂.,

Khao Luang, Nakhon Si Thamrat, 1,300 feet, c. 8° 26′ N., 99° 58′ E. 1 ♂, 1 ♀ (young).

Ellerman and Morrison-Scott (1951 : 101) do not include Thailand in the distribution of *M. minimus* although the species is listed by these authors from Tenasserim. However, Horsfield (1851 : 29) lists a specimen in the Museum of the East India Company collected in Thailand by Finlayson, apparently the same specimen listed subsequently from the Indian Museum by Anderson (1881 : 107), and Bonhote (1903 : 15) records a specimen from Patani, in southern Thailand.

Taphozous theobaldi theobaldi Dobson, 1872

THAILAND: Sara Buri. 1 ♂.

Khao Lom Phat, 21 kilometres eastnortheast of Sara Buri. 1 ♀.

Described from Tenasserim, *T. theobaldi* was listed from Thailand by Pousargues (1904 : 544) and has been recorded subsequently from North Vietnam (Bourret, 1944 : 9) and South Vietnam (Van Peenen, Ryan and Light, 1969 : 50). Measurements (♂, ♀): length of forearm 74·0, 74·1; greatest length of skull 24·2, 23·6; condylocanine length 23·9, 23·5; least interorbital width 7·5, 7·0; postorbital width 5·2, 5·3; zygomatic width 14·3, 14·1; braincase width 10·8, 11·1; mastoid width 12·8, 12·6; c^1–c^1 4·9, 4·8; m^3–m^3 10·2, 10·1; c–m^3 10·7, 10·5; length of mandible 18·7, 18·5; c–m_3 11·8, 11·7.

Taphozous longimanus longimanus Hardwicke, 1825

CAMBODIA: Prek Phnau, 6 kilometres northeast of Phnom Penh. 2 ♀♀.

Cambodia, no certain locality. 5 ♀♀.

Taphozous longimanus has not hitherto been reported from Cambodia although known to occur in Tenasserim (Wroughton, 1915 : 706) and further north in Burma (Wroughton and Davidson, 1918 : 477, Wroughton, 1918b : 25). The wings of these specimens are dusky, and they are referred to the nominate subspecies rather than to the pale-winged *T.l. albipinnis* from the Malay Peninsula, Sumatra and Borneo. Length of forearm 62·0, 62·3: of five females of uncertain provenance 60·5–63·1 (61·5).

Rhinolophus affinis macrurus Andersen, 1905

THAILAND: Doi Inthanon, Chom Thong, Chiangmai, 18° 35′ N., 98° 29′ E. 1 ♂.

Ban Papae, Mae Sariang, Mae Hong Son, 2,365 feet, c. 18° 45′ N., 97° 55′ E. 1 ♂. Now Senckenberg Museum No. 33816.

Longer tails (c. 26–29 mm.) refer these specimens to *R. a macrurus* rather than to *R. a superans* from the Malay Peninsula.

Rhinolophus malayanus Bonhote, 1903

THAILAND: Phu Nam Tok Tap, Kwang, Kaeng Koi, Sara Buri c. 14° 12′ N., 100° 52′ E. 1 ♀.

First described from Biserat, in Jalor, southern Thailand, the range of this species has since been extended to include Perlis, in the northern States of Malaya (Hill, in press), Pulau Langkawi, off the west coast of the Malay Peninsula (Hill, in press), Koh Lak, off the east coast of southern Thailand (Gyldenstolpe, 1916 : 13); Laos (Andersen, 1905: 89, Tate and Archbold, 1939: 6; Phillips, 1967: 634) and tentatively North Vietnam (Osgood, 1932 : 218). Measurements of the specimen from Sara Buri: length of forearm 40·1: greatest length of skull 18·3; greatest length to canine 17·3; condylocanine length 15·2; supraorbital length (distance from junction of supraorbital ridges to median anterior point of nasal swellings) 5·0; least interorbital width 1·9; zygomatic width 8·7; braincase width 7·4; mastoid width 8·3; c^1–c^1 4·2; m^3–m^3 6·4; c–m^3 6·7; length of mandible 11·3; c–m_3 7·0.

Phillips (1967 : 634) considers that on the basis of the published description it is probable that *Rhinolophus chaseni* Sanborn, 1939 from Con Son Island (Pulo Condore), off the southeastern coast of South Vietnam will prove conspecific with *R. malayanus*. Elsewhere, one of us (Hill, in press) has indicated that *chaseni* (probably the bat reported from Con Son as *R. minor* by Pousargues, 1904 : 544) is not closely related to *malayanus* as was suggested by its describer but instead should be considered a subspecies of *R. borneensis*. *Rhinolophus malayanus* differs from *R. borneensis* chiefly in the form of the anterior nasal swellings: in *malayanus* the median swellings are large and much inflated, extending laterally down the sides of the rostrum to the extent that the lateral swellings are relatively small, while in *borneensis* the median swellings are smaller and less inflated, not extending laterally down the sides of the rostrum, with the lateral swellings conspicuously larger than in *malayanus*. Examination of the holotype of *chaseni* shows it to belong with *borneensis* rather than with *malayanus*.

Rhinolophus shameli Tate, 1943

THAILAND: Ban Bon Dan, kilometre 58, Route 23, Korat, 400 metres. 1 ♂.

CAMBODIA: Preah Khan, Siem Reap, 3 ♂♂. 1 ♀.

Shamel (1942 : 319) referred two specimens from Thailand in the Smithsonian Institution to *R. coelophyllus* Peters, 1867, a species rare in collections and characterized by the unique hood-like appearance of the posterior nose-leaf, the connecting process entering a vertical fissure in its anterior face. The two specimens reported by Shamel, however, differed sufficiently from each other in a number of respects that this author described them individually. Subsequently, Tate (1943 : 2) considered that one, from the island of Chang in the Gulf of Siam, merited subspecific separation as *R.c. shameli* when compared with the other specimen, obtained at Chiangmai in northern Thailand. Apart from these specimens, *R. coelophyllus* has been reported from the Salween River (the type locality); from Tsagine (Sagain), Upper Burma (Ellerman and Morrison-Scott, 1951 : 123); from Koh Lak off the

east coast of southern Thailand (Gyldenstolpe, 1911 : 16) and from the States of Malaya (Chasen, 1940 : 42). The specimens now reported from Thailand and Cambodia, however, together with others obtained recently on Pulau Langkawi, off the west coast of the Malay Peninsula, suggest that *shameli* represents a distinct species.

According to Shamel (1942 : 319) the specimen from Koh Chang (*shameli*) is much more brightly coloured than that from Chiangmai and differs also in the configuration of the upper surface of the rostrum, which posteriorly to the nasal swellings is flat and not excavated, the margins formed by the division and forward extension of the sagittal crest not ridged or beaded. In the specimen from Chiangmai this region is scooped out, the margins of this depression formed by strong, beaded supraorbital ridges developed from the forward extension and division of the sagittal crest. Tate (1943 : 3) in describing the specimen from Koh Chang as *shameli* points out that it is considerably larger than the example from Chiangmai, as can be seen from the measurements published by Shamel, and also that it has hyopsodont teeth, these features together with its more brilliant coloration forming the basis of his diagnosis.

The specimen reported here from Ban Bon Dan agrees closely in colour with the description by Shamel (1942 : 319) of the example from Koh Chang subsequently designated as the holotype of *shameli* by Tate. The head is dark brown to the anterior bases of the ears: the remainder of the dorsal surface is bright golden brown, anteriorly slightly more brilliant, posteriorly a little browner. The individual hairs are pale cream for most of their length, tipped with the brighter colour. The ventral surface is paler, overall orange buff, lacking brown, the hairs orange buff at the base and for most of their length, with brighter tips. Cranially, the specimen agrees exactly with the description by Shamel of the Koh Chang example, the upper surface of the rostrum flat and not margined by prominent supraorbital ridges.

Specimens from Cambodia (whence neither *coelophyllus* nor *shameli* have been reported hitherto) and Upper Burma agree in size and rostral features with *shameli* but differ in colour. These specimens are brown dorsally, the individual hairs pale greyish white at the base: the ventral surface by contrast is very much paler, the throat, chest and belly pale buff, the hairs creamy white at the base and tipped with buff or buff brown. The flanks and inguinal region are slightly darker, the hair tips brown and lacking any buff. Since in all other respects these specimens agree exactly with *shameli* they support the view that this species exists in a brownish phase and a contrasting brighter, more reddish phase, a phenomenon not uncommon in *Rhinolophus*.

The collections of the British Museum (Natural History) include one example from Kedah and two from Pulau Langkawi which agree closely in colour with the specimens from Cambodia and Upper Burma referred here to *shameli* and with the description of a single specimen from Chiangmai reported by Shamel (1942 : 319): those from Langkawi (in alcohol) are very slightly browner ventrally than those from Cambodia. However, the three specimens are very much smaller than *shameli* and the upper surface of the rostrum is in each deeply excavated behind the nasal swellings, the depression enclosed laterally by prominent supraorbital ridges formed

from the anterior division of the sagittal crest, while all have less massive teeth. In these respects, they thus resemble precisely the specimen described from Chiangmai by Shamel which Tate (1943 : 3) noted was 'probably referable to the type from Salween River, Burma'. The type specimen of *coelophyllus* is small (forearm length 42, according to Peters, 1867a : 427) and for the present this name is used for the smaller species to which the Chiangmai, Kedah and Langkawi specimens belong. Those from Koh Lak reported by Gyldenstolpe (1911 : 16) are cranially a little smaller and may represent an undescribed subspecies of *R. coelophyllus* as Tate (p. 3) suggests. Measurements of *R. shameli* and *R. coelophyllus* are compared in Table 1.

Rhinolophus acuminatus Peters, 1871

THAILAND: Chonburi, 13° 22′ N., 100° 59′ E. 1 ♂, 2 ♀♀ (1 young).

Bang Phra, Siracha, Chonburi, 13° 12′ N., 100° 57′ E. 2 ♂♂ (1 now Senckenberg Museum No. 33817).

1 ♀ CAMBODIA: Preah Khan, Siem Reap. 3 ♂♂, 1 ♀.

Rhinolophus acuminatus is recorded from Thailand and Laos by Dobson (1878 : 878) and Pousargues (1904 : 544) and from Thailand by Shamel (1942 : 321) and Sanborn (1952 : 3): these specimens from Preah Khan constitute the first record of the species from Cambodia. Specimens from Thailand and Cambodia agree very closely in colour and size with an extensive series of *R.a. acuminatus* (to which Thai specimens are referred by Shamel and by Sanborn) from Java. Six examples (including three from Cambodia) are in the dark or grey phase, the dorsal pelage greyish brown, the hairs tipped light grey or silver, especially anteriorly: the ventral surface is pale grey. Three (including one from Cambodia) display the red or russet phase and are dorsally reddish brown, ventrally a little paler. A single example exhibits a condition midway between these extremes: the anterior part of the back is greyish brown, tinged with russet, the posterior back russet, while the ventral surface is suffused with russet yet retains much of its greyish tinge.

Although there is a good series of *R.a. acuminatus* in the British Museum (Natural History), the remaining subspecies, *R.a. audax* from Lombok, the Sumatran *R.a. sumatranus*, *R.a. calypso* from Enggano Island, off Sumatra and *R.a. circe* from nearby Nias Island are as yet only very poorly represented. Furthermore, Chasen and Kloss (1932 : 48) identify as *R. acuminatus* a specimen from Sabah, Borneo which Chasen (1940 : 39, footnote) suggested might represent an undescribed subspecies, provisionally associating it with *R.a. sumatranus*. Allen and Coolidge (1940 : 136) did not allocate specimens from Mount Kinabalu to subspecies, but Medway (1965 : 54) lists Bornean specimens as *R.a. sumatranus*. In these circumstances it is difficult to assess subspecific variation in *R. acuminatus* and for the present mainland specimens are left unallocated.

Rhinolophus borneensis Peters, 1861

CAMBODIA: Preah Khan, Siem Reap. 2 ♂♂.

There appears to be but one previous report of *R. borneensis* from the mainland of southeastern Asia, by Robinson and Kloss (1915b : 116), who tentatively identified

TABLE 1

Measurements of *Rhinolophus shameli, R. coelophyllus*

	Sex	Length of forearm	Greatest length of skull	Condylobasal length	Greatest length to canine	Condylocanine length	Width across nasal swellings	Rostral width	Least inter-orbital width	Zygomatic width	Braincase width	Braincase depth	Mastoid width	c^1–c^1	m^3–m^3	c–m^3	Length of mandible	c–m_3	Location
R. shameli																			
U.S.N.M.267255*	♂	46·2†	21·0	18·6	—	—	5·6	—	2·0	9·0	8·5	6·6	—	—	—	8·0†	—	8·5	Holotype. Koh Chang
9.1.4.14	♀	45·7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Upper Burma
76.5.26.2	♂	46·4	20·7	18·4	19·8	17·6	5·5	5·5	—	9·5	8·9	6·0	9·4	5·1	6·9	7·6	12·6	7·9	,, ,,
J.T. Marshall	♂	41·7	—	—	19·1	16·7	5·3	5·2	2·0	9·4	8·3	5·8	9·2	5·1	6·7	7·5	12·1	7·8	Korat, Thailand
Paris Mus.	♂	45·8	20·4	18·1	20·0	17·5	5·5	5·5	1·9	9·9	8·8	5·9	9·6	5·1	7·3	7·8	12·8	8·3	Cambodia
,, ,,	♂	46·2	19·9	18·1	19·5	17·4	—	5·3	1·8	9·9	8·4	6·0	9·4	4·8	7·2	7·8	—	8·1	,,
,, ,,	♂	46·2	20·7	18·6	20·1	17·7	5·5	5·4	2·1	9·9	8·7	5·7	9·6	4·8	7·1	7·9	—	8·3	,,
,, ,,	♀	46·4	20·7	18·5	20·0	17·7	5·4	5·3	1·8	9·7	8·6	5·8	9·5	5·0	7·0	7·5	—	8·1	,,
R. coelophyllus																			
U.S.N.M. 267260*	♂	41·0‡	19·0	17·5	—	—	5·2	—	2·0	9·0	8·2	5·2	—	—	—	7·5‡	—	7·6	Chiangmai, Thailand
98.10.1.1.	♂	42·9	—	—	18·8	16·3	4·9	4·8	2·2	9·5	8·3	5·6	9·2	4·6	6·6	7·2	11·9	7·5	Kedah
68.821	♀	42.7	19·4	17·2	18·7	16·7	5·0	4·9	2·1	9·4	8·6	5·8	9·2	4·7	6·7	7·3	—	7·6	Langkawi
68.822	♀	44·7	19·4	17·3	18·8	16·6	5·0	4·9	1·9	9·6	8·7	5·7	9·2	4·7	6·8	7·2	11·9	7·5	,,
Gyldenstolpe	♂	41·2	17·6	15·5	—	—	4·2	—	—	8·1	7·6	—	8·1	—	—	6·5	11·0	7·0	Koh Lak
,,	♀	41·4	17·8	—	—	—	4·7	—	—	8·1	—	—	8·1	—	—	6·8	—	7·0	,, ,,

* from Shamel

† Tate (1942 : 6) gives 46·0 and 8·5 for these values

‡ ,, ,, ,, 45·0 ,, 7·6 ,, ,, ,,

a specimen from Khao Nawng, Bandon, southern Thailand with this species. This specimen, however, later became the holotype of *R. robinsoni* Andersen, 1918. *Rhinolophus borneensis spadix* from the Natuna and Karimata Islands seems only barely separable (Andersen, 1905 : 87) from the Bornean subspecies *R.b. borneensis* by virtue of its very slightly larger ears. Both subspecies, like the Cambodian specimens, are a little larger in some respects than the holotype of *R.b. chaseni* Sanborn, 1939 (see above, under *R. malayanus*) from Con Son Island (Pulo Condore), but measurements of a series of *chaseni* given by Van Peenen, Ryan and Light (1969 : 59) and by Van Peenen, Cunningham and Duncan (1970 : 421) (in which by a lapsus the length of the forearm is given as the greatest skull length, the latter appearing as the zygomatic breadth) approach or overlap those of mainland specimens. It may well be, therefore, that *chaseni* will prove to be the correct subspecific name for the mainland population.

Specimens reported as *Rhinolophus* sp. from North Vietnam by Osgood (1932 : 219) seem perhaps referable to *R. borneensis*. In size they agree with those reported from Cambodia, and Osgood notes that the development of the nasal swellings is perhaps less than in *malayanus*, the skulls agreeing in general robustness with *stheno*. In *borneensis* the median nasal swellings are smaller than those of *malayanus* (see above, under *R. malayanus*), and, so far as mainland specimens are concerned, the skull is generally more robust, similar in this respect to *stheno*. Measurements of the Cambodian specimens, with those of the holotype of *R.b. chaseni* (in parentheses): length of forearm 44·1, 43·4, (41·3); greatest length of skull 19·7, 19·3 (18·7); condylocanine length 17·3; 17·6 (16·5): rostral width 5·3, 5·3, (5·3); width across nasal swellings 5·5, 5·5, (5·5); least interorbital width 2·5, 2·3 (2·5): zygomatic width 9·9, 9·9 (9·3); braincase width 8·3, 8·4 (8·2); mastoid width 9·5, 9·5, (8·8); c^1–c^1 4·8, 4·9 (4·9); m^3–m^3 7·2, 6·8, (6·8); c–m^3 7·7, 7·4, (7·3); length of mandible –, 12·7, –; c–m_3 8·3, 8·0, (7·8).

Coelops frithii Blyth, 1848

THAILAND: Khao Luang, Nakhon Si Thamrat, 1,300 feet, 8° 26′ N., 99° 58′ E. 1 ♂.

The elongate, narrow outline of the lappets projecting from the supplementary leaflets flanking the anterior noseleaf suggests that this specimen should be referred to *C. frithii* rather than to *C. robinsoni* in which these lappets are rounded and wider. Unfortunately, the skull, which would provide a more definite indication, is missing. Length of forearm 38·2.

Robinson and Kloss (1915b : 116) record two specimens from Khao Nawng, Bandon, southern Thailand as *C. robinsoni*. These, formerly in the collection of the Federated Malay States Museum (531/12, 532/12), are now in the collections of the British Museum (Natural History) (B.M. 68. 605–606). Elsewhere, one of us (Hill, in press), in a review of the species of *Coelops*, has shown these to be examples of *C. frithii*, which is recorded from Chiangmai by Gyldenstolpe (1916 : 15) and listed from Laos by Pousargues (1904 : 544).

Myotis hasseltii continentis Shamel, 1942

CAMBODIA: Prek Phnau, 6 kilometres northeast of Phnom Penh. 3 ♂♂, 3 ♀♀.

Large-footed *Myotis* of southeastern Asia stand in need of revision, but at the present time there is insufficient material in the collections of the British Museum (Natural History) from a suitably wide range of localities for this to be undertaken in detail. Specimens attributed to the named forms *horsfieldii*, *hasseltii*, and *adversus* have been reviewed recently (Hill, in press) and there seems little doubt that *M. horsfieldii* (Temminck, 1840) must be considered a distinct species (Medway, 1965 : 60) on account of its small size, blackish coloration and narrow braincase when compared with *hasseltii* and *adversus*. *Myotis deignani* Shamel, 1942, from Chiangmai, northern Thailand seems likely to be a subspecies of *horsfieldii*. *Myotis hasseltii* (Temminck, 1840) applies apparently to larger specimens in which the pelage is short, the post-palatal extension short and lacking thin bony laminae to support the post-palatal spine, in which i^2 and i^3 are relatively massive, the second upper premolar (pm^3) is minute, usually intruded from the toothrow and the second lower premolar (pm_3) very small, intruded from the toothrow sometimes to the extent that pm_2 and pm_4 are in contact or nearly so. *Myotis adversus* (Horsfield, 1824) is characterized by dense, woolly pelage, a long post-palatal extension with thin bony laminae supporting the post-palatal spine, pm^3 less reduced, usually not much intruded from the toothrow and with pm_3 although reduced, in the toothrow or only very slightly intruded.

Myotis hasseltii is distributed from Ceylon, Thailand and Indochina to Malaya, Java and Borneo. Specimens from Thailand and Cambodia agree closely with the description of *Myotis adversus continentis* Shamel, 1942 : 323 which apparently is referable to *hasseltii* rather than to *adversus*. Shamel says 'fur velvety and short': pm^3 is crowded inwards, with pm^2 and pm^4 in contact, while pm_3 is small, but in the holotype standing in the toothrow. According to Medway (1965 : 62) *M.h. macellus* (Temminck, 1835) is the Bornean subspecies. *Myotis adversus* occurs in Java (*M.a. adversus*) and Borneo (*M.a. carimatae* Miller, 1906) east to Australia (*M.a. moluccarum* (Thomas, 1915)).

Minimum, maximum and mean length of forearm in five specimens of *M. hasseltii continentis* from Cambodia 36·8–39·2 (38·2); measurements of three skulls (♂, ♀♀): greatest length 15·3, 15·7, 15·8; condylobasal length 14·4, 14·6, 14·6; least interorbital width 4·2, 4·1, 4·0; zygomatic width 10·2, 9·9, 10·2; width of braincase 7·8, 7·6, 7·8; mastoid width 8·6, 8·4, 8·6; c^1–c^1 4·3, 4·3, 4·3; m^3–m^3 6·1, 6·2, 6·0; c–m^3 5·5; 5·6, 5·7; length of mandible –, 11·1, 10·9; c–m_3 6·1, 6·1, 6·2.

Myotis annectans (Dobson, 1871)

THAILAND: Doi Pui, Chiangmai, 1,250 metres. 1 ♀. Collected by Kitti Thonglongya and now in the Thai National Reference Collection.

Topal (1970a) has recently examined the holotype of *Pipistrellus annectans* Dobson, 1871: 213 from the Naga Hills, Assam, in the Indian Museum, Calcutta and concluded that despite the absence of the small second premolars ($pm\frac{3}{3}$) it should be referred to *Myotis*. Furthermore, Topal has concluded that it is synonymous

with *Myotis primula* Thomas, 1920 : 248 from Pashok, near Darjeeling, northeastern India, which it antedates by many years. A result of this conclusion is that the subgeneric name *Megapipistrellus* Bianchi, 1917 with type species *Pipistrellus annectans* Dobson must be transferred to *Myotis*. Apart from the original, the only other record of *P. annectans* seems to be the report by Schneider (1905 : 80) of three specimens identified by Leche from the Upper Langkat, Sumatra and at that time in the Zoological Institute of the University of Stockholm. Schneider gave no diagnostic features but subsequently the specimens were described in detail by Arnbäck-Christie-Linde (1909 : 574). They are, however, much too small to be referred to *annectans*.

The specimen from Chiangmai agrees exactly with the description of *Pipistrellus annectans* by Dobson and provides an opportunity to describe the coloration of the species, the holotype being in alcohol, and also to make a direct comparison with the holotype of *Myotis primula*. Dorsally, the Chiangmai specimen is rich dark chestnut brown, the individual hairs dark brown at the base, tipped with paler brown. The ventral surface, including the underside of the head and throat, is greyish for the most part, with brown underlay, the hairs dark brown at the base, heavily tipped with greyish white. The hair tips on the belly are ochraceous or orange to produce an orange yellow median patch. The pelage is rather long and woolly, extending slightly on to the endopatagium but hardly at all on to the uropatagium.

The face is densely hairy, excepting the nostrils and the areas around the lips and eyes, the pelage forming a dense fringe on the forehead. Ears translucent distally, less so proximally, of moderate size with rounded tips. The anterior margin of the ear is strongly convex proximally, less so distally, the posterior margin sharply concave just below the tip, becoming convex, slightly concave again near the base of the tragus, with a small antitragal lobe. The tragus is long and tapering, with an acute, rounded tip, its anterior margin slightly concave, the posterior margin convex and with a small rounded basal lobe. There is no post-calcarial lobe and the extreme tip of the tail is free of the membrane.

The skull has an elongate, uninflated braincase, relatively wide unconstricted interorbital region and slight sagittal crest. The rostrum is low and narrow anteriorly, with shallow median frontal sulcus and short, U-shaped anterior narial emargination. The large anteorbital forearm is separated from the orbit by a moderate bar of bone with a small upper subsidiary foramen within the orbit. The palate is sharply domed, narrowed anteriorly, with U-shaped anterior emargination and wide ligulate post-palatal spine. The inner upper incisor (i^2) is large, slightly longer than wide, with large anterior cusp and lower posterior cusp: i^3 is wider than long, transverse to the toothrow, with a heavy cusp rising from a narrow cingulum and separated from the canine by a narrow diastema. Lower incisors with no especial peculiarities, canines low, c^1 about the same height as pm^4, c_1 similarly about the same height from the cingulum as pm_4. Anterior upper premolar (pm^2) large, in toothrow, touching c^1 and pm^4: pm_2 not reduced or displaced, in contact with c_1 and pm_4. No trace of $pm\frac{2}{3}$ in either jaw. The specimen agrees precisely with the diagnosis by Dobson of *P. annectans*, which it obviously represents.

A direct comparison with the holotype and other material of *Myotis primula*

Thomas, 1920 shows exact agreement in almost every respect. The ears in *primula* are not translucent distally as they are in the Chiangmai specimen which is very slightly more orange ventrally than *primula* but in every other external feature there is complete correspondence. The skulls and teeth agree precisely excepting only for the presence of a minute $pm\frac{3}{3}$ in *primula:* its degree of intrusion, however, varies in the specimens examined and although in the holotype (B.M.16.3.25.30) the anterior ($pm\frac{2}{2}$) and posterior ($pm\frac{4}{4}$) premolars do not touch, in two others (B.M.20.7.27.2–3) these teeth are in contact or nearly so. There can be no doubt that *annectans* is in fact *primula* in which these teeth have never appeared: the ears and tragus of *annectans* and *primula* refer the taxon which they represent indubitably to *Myotis*, as Topal has concluded. Measurements of *M. annectans* from Chiangmai are compared with those of *M. primula* in Table 2.

TABLE 2

Measurements of *Myotis annectans*

	M. annectans ♀ Chiangmai, Thailand	'*M. primula*' ♂ Holotype B.M.16.3.25.30 Assam	'*M. primula*' ♂ B.M.20.7.27.2 Assam	'*M. primula*' ♀ B.M.20.7.27.3 Assam
Length of forearm	43·3	47·0	46·5	45·2
Greatest length of skull	17·0	17·3	16·7	—
Condylobasal length	16·4	16·7	15·9	—
Condylocanine length	15·3	15·6	14·9	—
Least interorbital width	4·2	4·3	4·3	4·2
Zygomatic width	11·2	11·5	—	—
Braincase width	8·0	8·4	8·6	7·8
Mastoid width	8·8	8·6	8·5	8·4
c^1–c^1	4·5	4·8	4·8	4·6
m^3–m^3	7·6	7·3	7·4	7·2
c–m^3	6·7	6·9	6·6	6·7
Length of mandible	12·3	12·7	—	—
c–m_3	7·3	7·3	7·1	7·2

Myotis siligorensis thaianus Shamel, 1942

THAILAND: Tham Tab Tao, Fang, Chiangmai. 2 ♂♂. Thai National Reference Collection.

These are apparently the first of *M.s. thaianus* to be reported since its description from Chiangmai by Shamel (1942 : 323). Measurements: length of forearm 31·7, 31·9; greatest length of skull 12·8, 12·7; condylobasal length 11·8, –; condylocanine length 11·1, –; least interorbital width 2·8, 2·9; zygomatic width 7·0; –; braincase width 5·8, 6·0; mastoid width 6·4, 6·6; depth of braincase 4·7, –; c^1–c^1 3·0, 3·0; m^3–m^3 4·6, 4·7; length of entire toothrow 5·4, 5·3; c–m^3 4·5, 4·4; length of mandible 8·4, 8·6; c–m_3 4·9, 4·8.

Pipistrellus cadornae Thomas, 1916

THAILAND: Petchabun, Thung Salang, Luang, 450 metres. 1 ♂. Thai National Reference Collection.

The first of this species to be reported from Thailand, this specimen is in excellent agreement with the holotype and with those reported from Upper Burma by Hill (1962 : 133). Measurements: length of forearm 33·2, greatest length of skull 13·6; condylobasal length 12·9, condylocanine length 12·6; least inteorbital width 3·7, width of braincase 6·7; mastoid width 7·5; c^1–c^1 4·5, m^3–m^3 5·7 c–m^3 4·5; c–m_3 4·7.

Hesperoptenus tickelli (Blyth, 1851)

THAILAND: Nakhon Rat Sima (= Ḳhorat). 1 ♀.

Hesperoptenus tickelli has been recorded hitherto from no further east than Bengal on the Asian mainland and from the Andaman Islands so that its presence in eastern Thailand represents a considerable extension of range. In colour this specimen agrees more closely with Indian examples than with specimens from Ceylon and the Andaman Islands, which are very slightly darker dorsally, especially on the hindback. Measurements: length of forearm 52·3; greatest length of skull 18·5; condylobasal length 18·3; least interorbital width 5·0; zygomatic width 14·1; width of braincase 9·9; mastoid width 11·1; c^1–c^1 6·3; m^3–m^3 9·2; c–m^3 7·4; length of mandible 14·1; c–m_3 8·0.

Hesperoptenus blanfordi (Dobson, 1877)

THAILAND: Khao Luang, Nakhon Si Thamrat, 450 feet. 8° 26′ N., 99° 58′ E. 1 ♂.

This rare species has been recorded once previously from Thailand, by Robinson and Kloss (1915b: 116), who listed a specimen from Khao Nawng, Bandon. Measurements of the specimen from Khao Luang: length of forearm 25·8, greatest length of skull 12·2; condylobasal length 11·6; least interorbital width 4·3; zygomatic width –; width of braincase 7·0; mastoid width 7·2; c^1–c^1 –; m^3–m^3 6·2; c–m^3 3·9; length of mandible 8·4; c–m_3 – .

Scotophilus kuhlii gairdneri Kloss, 1917

THAILAND: Koh Klet, Pak Klet, Nonburi, 11 miles north of Bangkok. 1 ♀.

There is some uncertainty in the literature as to the correct classification of Asian *Scotophilus*, but there are, however, several partial studies of the Asian species. Briefly discussed by Sody (1928 : 86), the Asian forms were reviewed in some detail by Tate (1942 : 283) while Shamel (1942 : 325) provided a succinct examination of specimens in the United States National Museum which has remained largely overlooked by subsequent authors More recently, Siddiqi (1961) reviewed the Indian and some southeast Asian forms, while Peterson (1968) has reviewed the outstanding problems in the genus so far as southeastern Asia is concerned

The consensus of opinion is that two species should be recognized, a larger and a smaller, sympatric in some places (excluding the very large *Scotomanes* (*Parascotomanes*) *beaulieui* Bourret, 1942 from North Vietnam, listed in *Scotophilus* by

Ellerman and Morrison-Scott, 1951 : 180 but considered synonymous with *Ia io* by Topal, 1970b : 342). Tate, Shamel and Siddiqi assign smaller specimens to *Scotophilus temminckii* Horsfield, 1824; larger specimens are referred to *S. heathi* Horsfield, 1831 by Tate and Siddiqi and to *S. kuhlii* Leach, 1822 by Shamel. Examination of specimens in the British Museum (Natural History) confirms this division into two size groups.

A major difficulty arises in the allocation of names to these groups through the uncertain status of *Scotophilus kuhlii* Leach, 1822, the type species of *Scotophilus*, neither its specific identity nor its locality having been satisfactorily established. The name was considered indeterminable by Sody, Tate (who suggested a further study of the type specimen) and Siddiqi: over the years it has been used both for the smaller and the larger species. However, Peters (1867b : 679) thought the juvenile type specimen to be an example of *S. temminckii* (Horsfield, 1824), a conclusion reiterated by Dobson (1875 : 368) and by Blanford (1888 : 267), who also noted that an examination of the specimen by Thomas showed its upper incisors to be like those of *temminckii*. The type specimen was re-examined recently at the request of Dr R. L. Peterson, of the Royal Ontario Museum, who has published in part (1968 : 1081) the results of this survey. In brief, the holotype consists of a skull and specimen in alcohol, labelled India. It is a very young individual, the third upper molar just piercing the gum, with the two tricuspid milk incisors still present on each side of the jaw. On the right the unicuspid permanent incisor is emergent alongside the inner of these: on the left the permanent tooth has been lost from the damaged socket, only the two milk incisors remaining. Specimens of similar age in the collections of the British Museum (Natural History) are very like this, and the holotype seems at one of the normal stages of dental development in the genus. The dimensions of the teeth indicate that it represents the smaller of the two Asiatic species under consideration. The available evidence suggests that it originated from India: the name *kuhlii* should therefore replace *temminckii* for the smaller species, while *wroughtoni* Thomas, 1897, hitherto considered the Indian subspecies, will become a synonym of *S.k. kuhlii*. Siddiqi (1961 : 452 listed *castaneus* Gray, 1838 from West Bengal, East Pakistan to southwestern China and the Malay Peninsula. This author, however, did not examine *gairdneri* Kloss, 1917 from Thailand. Subspecies allocated to *kuhlii* are listed in full by Tate (1942 : 285) and Shamel (1942 : 327): for the present *gairdneri* is retained for Siamese and Cambodian specimens on account of their slightly darker dorsal coloration when compared with Indian specimens (*kuhlii*): *castaneus* from the Malay Peninsula is dorsally similar to *gairdneri* but is darker ventrally. There is a wide degree of individual colour variation, however, and these differences are small: at best it seems that the subspecies are only weakly separable. Length of forearm (eight specimens) 49·1–51·2 (50·3).

Scotophilus heathi (?) *watkinsi* Sanborn, 1952

THAILAND: Bang Phra, Siracha, Chonburi, 13° 12′ N., 100° 57′ E. 1 ♂.
Koh Klet Pak Klet, Nonburi, 11 miles north of Bangkok. 1 ♀.
Bangkok. 1 sex uncertain (skull only).

The collections of the British Museum (Natural History) include extensive series of *S. heathi* from Indian and Burmese localities (listed by Wroughton (1918a : 594) as *S. kuhlii*) but the representation from Thailand and Indochina is very much poorer. As in *S. kuhlii*, there is considerable individual colour variation and for the present no attempt has been made to determine subspecific boundaries.

These specimens are similar in size to those from Pak Nam Pho, Nakon Sawan Province, central Thailand described as *S. solutatus watkinsi* by Sanborn (1952 : 4) to which they are provisionally referred. The description and measurements lead this to be allocated to *S. heathi*, and it may represent a valid subspecies in Thailand.

Measurements (♂, ♀, sex uncertain): length of forearm 61·2, 61·4, –; greatest length of skull 22·6, 22·5, 22·0; condylobasal length 20·8, 20·9, 20·3; palatal length 7·7, 7·8, 7·6; rostral width between anteorbital foramina 8·3, 8·3, 7·9; least interorbital width 5·4, 5·3, 5·3; zygomatic width 16·4, 16·5, 15·9; mastoid width 14·2, 14·4, 13·8; braincase width 10·6, 10·7, 10·2; c^1–c^1 7·6, 7·7, 7·4; m^3–m^3 10·3, 10·2, 9·8; c–m^3 7·6, 7·7, 7·5; length of mandible 15·5, 16·0, 15·3; c–m_3 8·8, 8·9, 8·7.

Murina cyclotis cyclotis Dobson, 1872

THAILAND: Tham Tab Tao, Fang, Chiangmai. 1 ♂ (young adult).

The genus *Murina* was recorded from Thailand by Shamel (1942 : 327) who identified two specimens from the northern part of the country as *M. toxopei* Thomas, 1923 (= *M. florium toxopei*) known otherwise from the island of Buru, in the Moluccas. This specimen from Chiangmai is quite clearly referable to *M. cyclotis cyclotis* as it is described by Hill (1963 : 53), agreeing closely with specimens in the British Museum (Natural History) from northern Burma. It is probable that the specimens described and measured by Shamel also represent *M.c. cyclotis* with which from the account they agree in most respects.

Tadarida plicata plicata (Buchanan, 1800)

THAILAND: Phu Nam Tok Tap Kwang, Kaeng Khoi, Sara Buri, c. 14° 42′ N., 100° 52′ E. 1 ♂.

CAMBODIA: Angkor Wath, Siem Reap, Cambodia. 1 ♀.

Tonle, 25 kilometres southeast of Phnom Penh, Cambodia. 1 ♂, 5 ♀♀.

Yoshiyuki (1966 : 40) reported *T.p. plicata* for the first time from Cambodia. Length of forearm in the Thai example 47·7; in specimens from Cambodia 46·9–49·0 (48·0).

SUMMARY

Collections of bats from Thailand and Cambodia examined recently at the British Museum (Natural History) have included a number of species new to these countries or of taxonomic significance. *Megaerops ecaudatus*, *Chironax melanocephalus*, *Myotis annectans*, *Pipistrellus cadornae* and *Hesperoptenus tickelli* are reported for the first time from Thailand, together with *Pteropus hypomelanus* from the islet of Koh Som in the South China Sea. The first specimens of *Taphozous longimanus*

longimanus, *Rhinolophus borneensis* and *R. acuminatus* from Cambodia are recorded, with further examples of *Tadarida plicata plicata*, known hitherto in that country from one reported occurrence. Further specimens reported of species poorly known from Thailand include *Rousettus amplexicaudatus*, *R. leschenaulti leschenaulti*, *Sphaerias blanfordi*, *Macroglossus minimus sobrinus*, *Taphozous theobaldi theobaldi*, *Rhinolophus malayanus*, *R. acuminatus*, *Coelops frithii*, *Myotis hasseltii continentis*, *M. siligorensis thaianus*, *Hesperoptenus blanfordi* and *Murina cyclotis cyclotis*. An examination of *Cynopterus angulatus* Miller, 1908 shows it to be a subspecies of *C. sphinx* rather than of *C. brachyotis*. Further specimens of *Rhinolophus coelophyllus shameli* Tate, 1942 indicate that *shameli* is specifically distinct from *R. coelophyllus*. *R. chaseni* Sanborn, 1939 is thought to be a subspecies of *R. borneensis*. Large-footed *Myotis* of southeastern Asia are discussed and *continentis* Shamel, 1942 thought to be a subspecies of *M. hasseltii* rather than of *M. adversus* as it was described. A specimen referable to *Pipistrellus annectans* Dobson, 1871 confirms the view that this taxon should be referred to *Myotis* and that *M. primula* Thomas, 1920 is its synonym. The holotype of *Scotophilus kuhlii* Leach, 1822 has been examined and this name applied to the smallest of the Asiatic species of *Scotophilus*, formerly referred to *S. temminckii* (Horsfield, 1824).

REFERENCES

Allen, G. M. & Coolidge, H. J. 1940. Mammal and bird collections of the Asiatic Primate Expedition. 3. Mammals. *Bull. Mus. Comp. zool. Harv.* **87** : 131–166.

Andersen, K. 1905. On some bats of the genus *Rhinolophus*, with remarks on their mutual affinities, and descriptions of twenty-six new forms. *Proc. zool. Soc. Lond.* **2** : 75–145, 22 figs., 2 pls.

—— 1912. *Catalogue of the Chiroptera in the collection of the British Museum. I. Megachiroptera.* London.

—— 1916. *In* Kloss, C. B. On a collection of mammals from the coast and islands of southeast Siam. With an account of the fruit bats, by Dr Knud Andersen. *Proc. zool. Soc. Lond.* 27–75, 1 pl.

—— & Kloss, C. B. 1915. Remarks on some races of *Cynopterus*. *J. fed. Malay St. Mus.* **5** : 220–222.

Anderson, J. 1881. *Catalogue of the Mammalia in the Indian Museum, Calcutta. Part I. Primates, Prosimiae, Chiroptera, and Insectivora.* Calcutta.

Ärnbäck-Christie-Linde, A. 1909. On intermediate forms among Chiroptera. *Zool. Anz.* **34** : 572–582, 4 figs.

Bhat, H. R. 1968. *Sphaerias blanfordi* (Thomas, 1891) from Himalayan region of Uttar Pradesh: an addition to the Chiropteran fauna of India. *J. Bombay nat. Hist. Soc.* **65** : 471–473, 1 tab.

Blanford, W. T. 1888. Notes on Indian Chiroptera. *J. Asiat. Soc. Beng.* **57,** (2) : 260–272.

Bonhote, J. L. 1903. Anthropological and Zoological results of an expedition to Perak and the Siamese Malay States, 1901–1902. Undertaken by Nelson Annandale and Herbert C. Robinson. Report on the mammals. *Fasciculi Malayenses* **1** : 1–44, 4 pls.

Bourret, R. 1944. Mammifères récemment entrés dans les collections du laboratoire de zoologie de l'Ecole Superieure des Sciences – description d'une varieté nouvelle. *Notes Trav. Ec. sup. Sci. Hanoi* **3** : 1–17.

Chasen, F. N. 1940. A handlist of Malaysian mammals. *Bull. Raffles Mus.* No. 15: 1–xx, 1–209, map.

—— & Kloss, C. B. 1932. Mammals from lowlands and islands of North Borneo. *Bull. Raffles Mus.* No. 6 (1931) : 1–82.

DOBSON, G. E. 1871. Notes on nine species of Indian and Indo-Chinese Vespertilionidae, with remarks on the synonymy and classification of some other species of the same family. *Proc. Asiat. Soc. Beng.* 210–215.

—— 1875. On the genus *Scotophilus*, with description of a new genus and species allied thereto. *Proc. zool. Soc. Lond.* 368–373.

—— 1878. Notes on recent additions to the collection of Chiroptera in the Muséum d'Histoire Naturelle at Paris, with descriptions of new and rare species. *Proc. zool. Soc. Lond.* 873–880.

ELLERMAN, J. R. & MORRISON-SCOTT, T. C. S. 1951. *Checklist of Palaearctic and Indian mammals, 1758–1946.* 1st. ed. London.

GYLDENSTOLPE, N. 1916. Zoological results of the Swedish Zoological Expeditions to Siam 1911–1912 & 1914–1915. *K. svenska Vetensk Akad. Handl.* **57**, (2) : 1–59, 6 pls.

HORSFIELD, T. 1851. *A catalogue of the Mammalia in the Museum of the Hon. East-India Company.* London.

HILL, J. E. 1961. Fruit-bats from the Federation of Malaya. *Proc. zool. Soc. Lond.* **136** : 629–642, 1 fig., 4 tabs.

—— 1962. Notes on some insectivores and bats from Upper Burma. *Proc. zool. Soc. Lond.* **139** : 119–137, 5 tabs.

—— 1963. Notes on some tube-nosed bats, genus *Murina*, from southeastern Asia, with descriptions of a new species and a new subspecies. *Fedn. Mus. J.* N.S. **8** : 48–59, 4 pls.

—— (in press). New records of Malayan bats, with taxonomic notes and the description of a new *Pipistrellus*. *Bull. Br. Mus. nat. Hist.* (Zool.) **23** : 21–42, 3 tabs.

KLOSS, C. B. 1911. On a collection of mammals and other vertebrates from the Trengganu Archipelago. *J. Fed. Malay St. Mus.* **4** : 175–212.

—— 1916. On a collection of mammals from the coast and islands of south-east Siam. With an account of the fruit-bats, by Dr. Knud Andersen. *Proc. zool. Soc. Lond.* 27–75, 1 pl.

—— 1917. On a third collection of Siamese mammals. *J. nat. Hist. Soc. Siam* **2** : 288–318.

—— 1919. On mammals collected in Siam. *J. nat. Hist. Soc. Siam* **3** : 333–407, 1 pl.

LINDSAY, H. M. 1927. Bombay Natural History Society's Mammal Survey of India, Burma and Ceylon. Report No. 39, Mergui Archipelago. *J. Bombay nat. Hist. Soc.* **31** : 42–48.

MARSHALL, J. & VANDEE, N. 1970. Mammals of Samui Island, Thailand. *Nat. Hist. Bull. Siam Soc.* **23** : 501–507, 1 pl., 1 tab.

MEDWAY, LORD. 1965. Mammals of Borneo. Field keys and an annotated checklist. *J. Malay. Brch R. Asiat. Soc.* **36**, (1963) : i–xiv, 1–193, 9 figs., 34 pls., 5 tabs., map.

—— 1969. *The wild mammals of Malaya and offshore islands including Singapore.* Kuala Lumpur; Singapore; London.

MILLER, G. S. 1898. List of bats collected by Dr. W. L. Abbott in Siam. *Proc. Acad. nat. Sci. Philad.* 316–325.

—— 1906. Seven new Malayan bats. *Proc. biol. Soc. Wash.* **19** : 61–65.

OSGOOD, W. 1932. Mammals of the Kelley–Roosevelts and Delacour Asiatic Expeditions. *Publs. Field Mus. nat. Hist.* (Zool. Ser.) **18** : 193–339, 30 figs., 2 pls.

PETERS, W. 1867a. On some mammals collected by Capt. A. C. Beavan, C.M.Z.S., at Moulmein, Burmah. *Proc. zool. Soc. Lond.* (1866) : 426–430, 1 pl.

—— 1867b. Fernere Mittheilungen zur Kenntnifs der Flederthiere namentlich über Arten des Leidener und Britischen Museums. *Mber. k. preuss. Akad. Wiss.* (1866) : 672–681.

PETERSON, R. L. 1968. Notes on an unusual specimen of *Scotophilus* from Vietnam. *Can. J. Zool.* **46** : 1079–1081, 1 fig.

PHILLIPS, C. J. 1967. A collection of bats from Laos. *J. Mammal.* **48** : 633–636, 1 tab.

POUSARGUES, E. DE. 1904. *Mammifères de l'Indo-Chine. In* Pavie, A.J.M. *Mission Pavie Indo-Chine* 1879–1895. *Études Diverses. III Recherches sur l'Histoire Naturelle de l'Indo-Chine Orientale.* Paris.

ROBINSON, H. C. & KLOSS, C. B. 1915a. The zoology of Koh Samui and Koh Pennan. *J. fed. Malay St. Mus.* **5** : 128–152.

ROBINSON, H. C. & KLOSS, C. B. 1915b. On a collection of mammals from the Siamese Province of Bandon, N.E. Malay Peninsula. *J. fed. Malay St. Mus.* **5** : 111–127.

—— 1918. Results of an expedition to Korinchi Peak, Sumatra I. Mammals. *J. fed. Malay St. Mus.* **8** (2) : 1–80, 1 pl.

SANBORN, C. C. 1952. The mammals of the Rush Watkins Zoological Expedition to Siam. *Nat. Hist. Bull. Siam. Soc.* **15** : 1–20.

SCHNEIDER, G. 1905. Ergebnisse zoologischer Forschungsreisen in Sumatra. Säugetiere (Mammalia). *Zool. Jb. (Syst.)* **23** : 1–172, 1 fig., 3 pls., 2 maps.

SHAMEL, H. H. 1942. A collection of bats from Thailand (Siam). *J. Mammal.* **23** : 317–328.

SIDDIQI, M. S. U. 1961. Notes on the status of bats of the genus *Scotophilus* from southern Asia with key to the recognized forms. *Ann. Mag. nat. Hist.* (13), **3**, (1960) : 449–454.

SODY, H. J. V. 1928. Twee nieuwe subspecies van *Pachyotis temminckii* Horsf. *Natuurk. Tijdschr. Ned.-Indië*, **88** : 86–91.

TATE, G. H. H. 1942. Results of the Archbold Expeditions. No. 47. Review of the Vespertilionine bats, with special reference to genera and species of the Archbold Collections. *Bull. Am. Mus. nat. Hist.* **80** : 221–297, 5 figs.

—— 1943. Results of the Archbold Expeditions. No. 49. Further notes on the *Rhinolophus philippinensis* group (Chiroptera). *Am. Mus. Novit.* No. 1219 : 1–7.

—— & ARCHBOLD, R. 1939. Results of the Archbold Expeditions. No. 24. Oriental *Rhinolophus*, with special reference to material from the Archbold Collections. *Am. Mus. Novit.* No. 1036 : 1–12, 1 tab.

THOMAS, O. 1920. Scientific results from the Mammal Survey. No. XXIII. A new bat of the genus *Myotis* from Sikkim. *J. Bombay nat. Hist. Soc.* **27** : 248–249.

TOPAL, G. 1970a. On the systematic status of *Pipistrellus annectans* Dobson 1871 and *Myotis primula* Thomas 1920 (Mammalia). *Annls hist.-nat. Mus. natn. hung.* Zool. **62** : 373–379, 2 tabs.

—— 1970b. The first record of *Ia io* Thomas, 1902 in Vietnam and India, and some remarks on the taxonomic position of *Parascotomanes beaulieui* Bourret, 1942, *Ia longimana* Pen, 1962 and the genus *Ia* Thomas, 1902 (Chiroptera, Vespertilionidae). *Opusc. zool. Bpest* **10** : 341–347, 2 figs., 2 tabs.

VAN PEENEN, P. F. D., RYAN, P. F. & LIGHT, R. H. 1969. *Preliminary Identification Manual for mammals of South Vietnam.* Washington.

——, CUNNINGHAM, M. L. & DUNCAN, J. F. 1970. A collection of mammals from Con Son Island, Vietnam. *J. Mammal.* **51** : 419–424, 1 fig.

WROUGHTON, R. C. 1915. Bombay Natural History Society's Mammal Survey of India, Burma and Ceylon. Report No. 17. South Tenasserim. *J. Bombay nat. Hist. Soc.* **23** : 695–720.

—— 1918a. Summary of the results from the Indian Mammal Survey of the Bombay Natural History Society. *J. Bombay nat. Hist. Soc.* **25** : 547–598.

—— 1918b. Summary of the results from the Indian Mammal Survey of the Bombay Natural History. *J. Bombay nat. Hist. Soc.* **26** : 19–58.

—— & DAVIDSON, W. M. 1918. Bombay Natural History Society's Mammal Survey of India, Burma and Ceylon. Report No. 29. Pegu. *J. Bombay nat. Hist. Soc.* **25** : 472–481.

YOSHIYUKI, M. 1966. On *Tadarida plicata plicata* newly collected from Cambodia. *J. mammal Soc. Japan* **3** : 40–42.

J. E. HILL
Department of Zoology
BRITISH MUSEUM (NATURAL HISTORY)
CROMWELL ROAD
London, SW7 5BD

KITTI THONGLONGYA
THAI NATIONAL REFERENCE COLLECTION
APPLIED SCIENTIFIC RESEARCH CORPORATION OF THAILAND
196, PHAHON YOTHIN ROAD
BANG KHEN, BANGKOK – 9

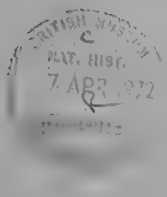
A LIST OF SUPPLEMENTS TO THE ZOOLOGICAL SERIES OF THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY)

1. KAY, E. ALISON. Marine Molluscs in the Cuming Collection British Museum (Natural History) described by William Harper Pease. Pp. 96; 14 Plates. 1965. (Out of Print.) £3.75.
2. WHITEHEAD, P. J. P. The Clupeoid Fishes described by Lacepede, Cuvier and Valenciennes. Pp. 180; 11 Plates, 15 Text-figures. 1967. £4.
3. TAYLOR, J. D., KENNEDY, W. J. & HALL, A. The Shell Structure and Mineralogy of the Bivalvia. Introduction. Nuculacea-Trigonacea. Pp. 125; 29 Plates, 77 Text-figures. 1969. £4.50.
4. HAYNES, J. R. Cardigan Bay recent Foraminifera (Cruises of the R.V. *Antur*) 1962–1964. (*In press.*)

Printed in England by Staples Printers Limited at their Kettering, Northants, establishment

A REDESCRIPTION OF *SPELAEOMYSIS SERVATUS* (FAGE) COMB. NOV. (MYSIDACEA : LEPIDOMYSIDAE) FROM THE MATERIAL COLLECTED ON ALDABRA ATOLL,

WITH A KEY TO THE SPECIES OF LEPIDOMYSIDAE



R. W. INGLE

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 22 No. 7
LONDON : 1972

A REDESCRIPTION OF *SPELAEOMYSIS SERVATUS* (FAGE) COMB. NOV. (MYSIDACEA : LEPIDOMYSIDAE) FROM THE MATERIAL COLLECTED ON ALDABRA ATOLL,

WITH A KEY TO THE SPECIES OF LEPIDOMYSIDAE

BY

RAYMOND WILLIAM INGLE

Pp 197–210; 5 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 22 No. 7
LONDON : 1972

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY) *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at regular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 22 *No.* 7 *of the Zoological series. The abbreviated titles of periodicals cited follow those of the World List of Scientific periodicals.*

World List abbreviation
Bull. Br. Mus. nat. Hist. (Zool.).

© Trustees of the British Museum (Natural History), 1972

TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 30 *March*, 1972 *Price* 65p

A REDESCRIPTION OF *SPELAEOMYSIS SERVATUS* (FAGE) COMB. NOV. (MYSIDACEA: LEPIDOMYSIDAE) FROM THE MATERIAL COLLECTED ON ALDABRA ATOLL,

WITH A KEY TO THE SPECIES OF LEPIDOMYSIDAE

By R. W. INGLE

SYNOPSIS

The crustacean *Spelaeomysis servatus* (Fage) is redescribed from specimens collected on Aldabra Atoll. The species has been transferred from the genus *Lepidomysis* Clarke. A key is provided for the identification of the known species in the genus *Spelaeomysis*.

INTRODUCTION

Among the crustaceans collected by Dr. K. G. McKenzie during phase III of the Royal Society of London Expedition to Aldabra (see McKenzie, 1971), were a number of mysidaceans that agree substantially with the descriptions and figures by Fage (1924, 1925) of a species designated by him as *Lepidophthalmus servatus*. For nomenclatorial reasons the generic name used by Fage was replaced by *Lepidops* (Zimmer, 1927) and later by *Lepidomysis* (Clarke, 1961). The type material of this species is from S. Zanzibar, E. Africa. As far as I am aware this material from Aldabra constitutes the second occurrence of this species and extends its range some 400 miles south eastward of the type locality.

Unlike the type material, these Aldabran specimens are well preserved. Adults and juveniles of both sexes are represented, although there are no ovigerous females in the sample. The opportunity has been taken, therefore, to redescribe the species from this fresh material and to compare it with the other known species of Lepidomysidae, *Spelaeomysis bottazzii* Caroli, 1924, *S. quinterensis* (Villalobos, 1951), and *S. longipes* Pillai and Mariamma, 1964. These comparisons have shown that *Lepidomysis* cannot be retained as a separate genus and that *L. servatus*, the only species in the genus, must be transferred to *Spelaeomysis*. The reasons for this decision are discussed on p. 207. The definition of the genus *Spelaeomysis* is amended slightly and a key is provided to separate the species belonging to this genus.

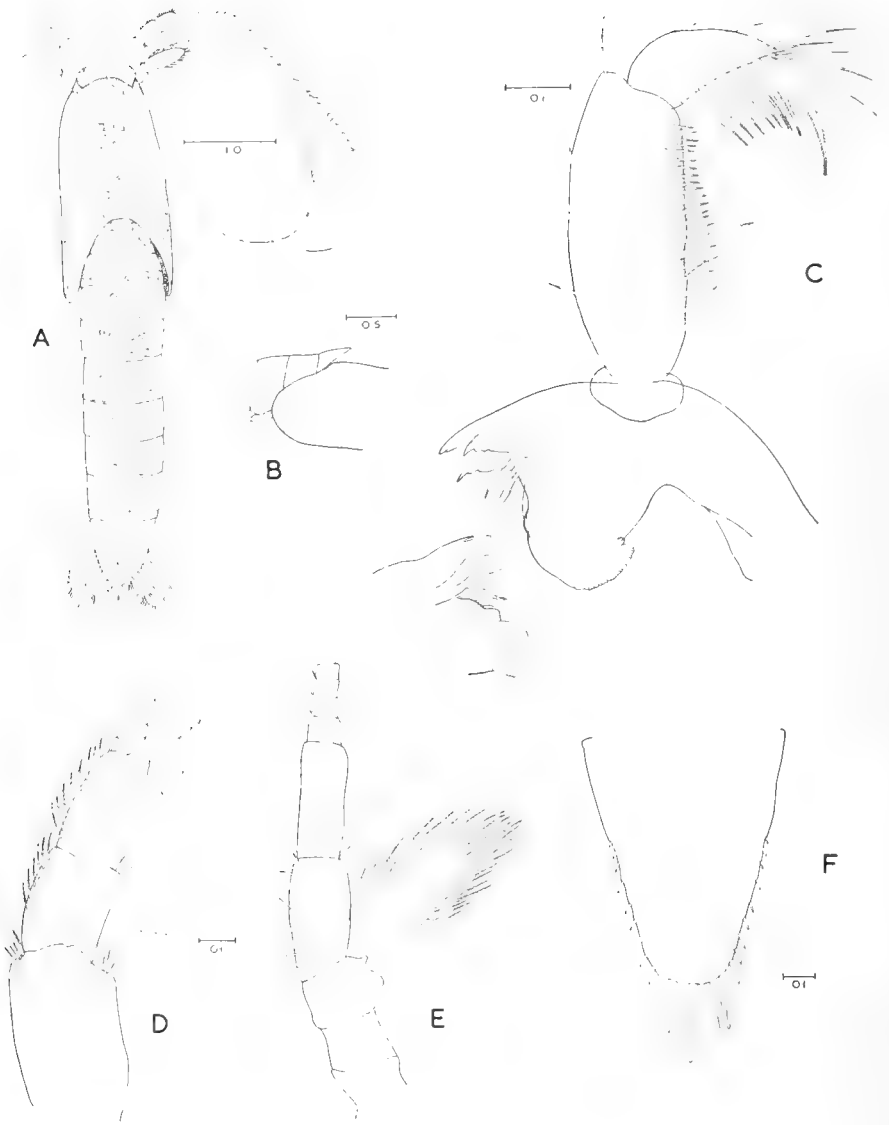


FIG. 1. *Spelaeomysis servatus* (Fage). Male, 5·5 mm, t.l. Aldabra Atoll. A. Dorsal view showing chromatophore pattern, thoracic limbs omitted. B. Lateral view showing projecting scale of penultimate thoracic segment. *C*. Left mandible, ventral aspect, lower inset – distal portion of right mandible. *D*. Right antennule, peduncle and proximal flagella segments, ventral aspect. *E*. Left antenna, peduncle and proximal flagellum segments, ventral aspect. *F*. Telson, dorsal aspect. Scales in mm.

SYSTEMATICS

Family **LEPIDOMYSIDAE** Clarke, 1961 : 251

Spelaeomysis servatus (Fage) comb. nov.

Lepidophthalmus servatus Fage, 1924 : 2127; 1925 : 525, figs 1–7.
Lepidops servatus; Zimmer, 1927 : 644; Gordon, 1960 : 299, 308, figs 20, 21, 27, 28.
Lepidomysis servatus; Clarke, 1961 : 251.

MATERIAL EXAMINED. 20 ♂♂, 3·0–5·5 mm, 17 ♀♀, 4·0–6·0 mm, (total lengths measured from distal margins of eyes to distal margins of telsons). Station 30, Aldabra Atoll, Indian Ocean, lat. 9° 24′ S., long. 46° 20′ E, local coordinates used by Royal Soc. Exped. 3755, 0525. Tide-dominated saline seepage pool in *Pemphis* scrub. Salinity 23·5°/oo. Associated fauna: *Cirolana sp.* marine molluscs, marine alga *Caulerpa verticillata.* Collected by Dr. K. G. McKenzie, 1.2.1968.

DESCRIPTION. *Male* (fig. 1*A*), body sub-cylindrical, carapace lateral margins strongly deflected ventrally, posterior expansions reaching to middle of first abdominal segment, antero-lateral expansions extending beyond rostral apex, rostrum broadly rounded. Carapace with a pair of faint longitudinal grooves, extending forward from posterior margin of carapace to its middle and then strongly deflected ventrally. Last two thoracic segments dorsally exposed, penultimate segment with a well developed scale overlapping the postero-median carapace margin and shown in lateral aspect in fig. 1B. Outline of thoracic and abdominal segments continuous. First abdominal segment shortest, sixth segment longest. Postero-ventral margins of segments 3–5 each with a single broad lamella arising between the pleopod bases and increasing in size respectively on each segment. Telson (fig. 1F) linguiform, posterior margin with a long median spine flanked on either side by one short and two long spines; lateral margins unarmed proximally, but with a row of 9 or 10 spines in the distal two thirds, increasing in length posteriorly. Each eyestalk (eye-plate) flattened dorso-ventrally and sub-triangular, narrowing anteriorly with inner margin curved, the cornea well developed. Antennule (fig. 1*D*), first peduncular segment longer than second segment, third sub-equal to second, inner flagellum reaching to middle of third abdominal segment, outer flagellum slightly shorter than inner one and with aesthetascs on inner margins of segments, decreasing in length distally. Antenna (fig. 1*E*), sympod three-segmented, first to third segments incompletely separated, third segment with a sub-acute process on outer distal margin. Exopod (scale) sub-oval, about half as long again as first segment of endopod peduncle, whole margin of scale setosed except near base. Peduncle of endopod formed of two sub-equal segments, flagellum reaching to second abdominal segment. Labrum outline shown in fig. 2*D*. Left mandible (fig. 1*C*), with a strongly bifid incisor process, each bifurcation faintly dentate, lacinia mobilis prominent and dentate, four penicils (spines) present, molar process truncate. Right mandible with lacinia mobilis bifid (inset to fig. 1*C*), and with molar process differing in shape from that of left mandible. Palp stout and three-segmented, first segment short, second longest and with pectinate and simple setae, distal segment narrowest and with long pectinate and simple setae. Maxillule (fig. 2*B*), proximal endite with five setae (three distal and two proximal) and four weakly

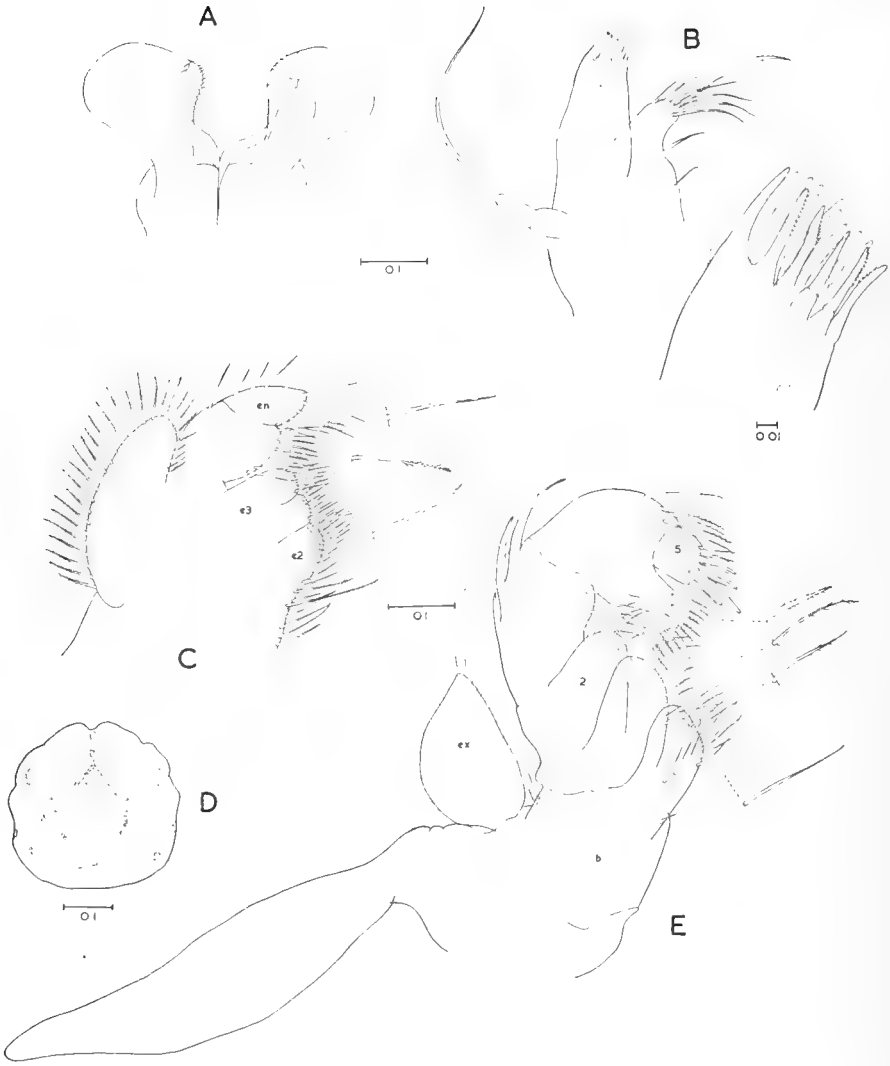


FIG. 2. *Spelaeomysis servatus* (Fage). Male, 5·5 mm. t.l. Aldabra Atoll. *A*. Labium. *B*. Right maxillule, right inset – distal portion of major lobe. *C*. Right maxilla. *D*. Labrum. *E*. First right thoracic limb. All from ventral aspect. Scales in mm.

pectinate long spines distally. Distal endite with three subterminal setae, fourteen or fifteen strong spines (some pectinate) and one or two simple setae. Maxilla (fig. 2*C*), exopod oval and with twenty nine or thirty long plumose setae, distal lobe well developed, proximal lobe undifferentiated, distal endopod segment (*en*) smaller than proximal segment, latter with a slightly expanded inner margin, endite of second segment (*e*2) of sympod and bifid endite of third segment (*e*3) well developed. Maxilla with simple and pectinate setae of types shown in insets to fig. 2*C*. Labium (fig. 2*A*), symmetrical and deeply cleft, inner margins of each lobe setose. First thoracic limb (fig. 2*E*), with coxa not clearly demarcated from basis (*b*), inner margin of basis expanded. First, second (2) and fourth endopod segments with inner margins expanded, fifth (5) segment truncate. Inner margin of fourth segment invested with a row of stout pectinate setae. Outer distal margin of third segment with three long spines, remaining segments of endopod with plumose or with simple setae as shown in figure. Exopod (*ex*) reduced to a lanceolate scale bearing two terminal setae and a row of fine short hair-like setae on both margins, epipod long. Second thoracic limb (fig. 3*A*), coxa demarcated from basis, first endopod segment almost as long as second segment, third segment longest, fourth longer than fifth. Inner margins of third to fifth segments with stout pectinate and plumose setae. Exopod well developed and nine-segmented, basal segment longest, seven distal segments each with a pair of plumose setae. Third, fourth, fifth and sixth thoracic limbs all similar in shape. Fifth limb (fig. 3*B*), with coxa not differentiated from basis, length of first endopod segment about one third the length of second segment, third segment about two and a half times length of second, fourth slightly shorter than third, claw about one fifth length of fifth segment. Exopod long, basal segment longest, ten distal segments (not shown in figure) each with a pair of long plumose setae. Seventh thoracic limb (fig. 3*C*) with coxa not differentiated from basis. First endopod segment slightly shorter than second (2), third almost three and a half times length of second, fourth slightly longer than third and with an outer proximal row of six pectinate setae, fifth segment about two thirds length of fourth, claw about half the length of fifth segment. Exopod slightly shorter than those on preceding limbs. Eighth thoracic limb (fig. 3*D*), with coxa slightly differentiated from basis. Coxal segment with inner broad setose penial lobe. First and second endopod segments equal in length, third segment about three and a half times the length of second, fourth much longer than third and with outer proximal row of seven and inner distal row of three pectinate setae, fifth segment shorter than fourth, inner margin with a row of fifteen long pectinate setae, claw almost half length of fifth segment. Exopod with distal segments not clearly differentiated.

First to fifth pleopods biramous and invested with plumose setae. Endopod one-segmented and increasing in length progressively from first to fifth pleopods. Exopods of pleopods three-segmented with first segment shortest. First pleopod (Fig. 4*A*) with second and third segments of exopods equal in length, second segment with a small longitudinal setose ridge on inner ventral surface. Second pleopod (fig. 4*B*), with second exopod segment longest and broadly expanded, inner margin with a proximal row of graded setae and a distal row of retinaculae; a ventral

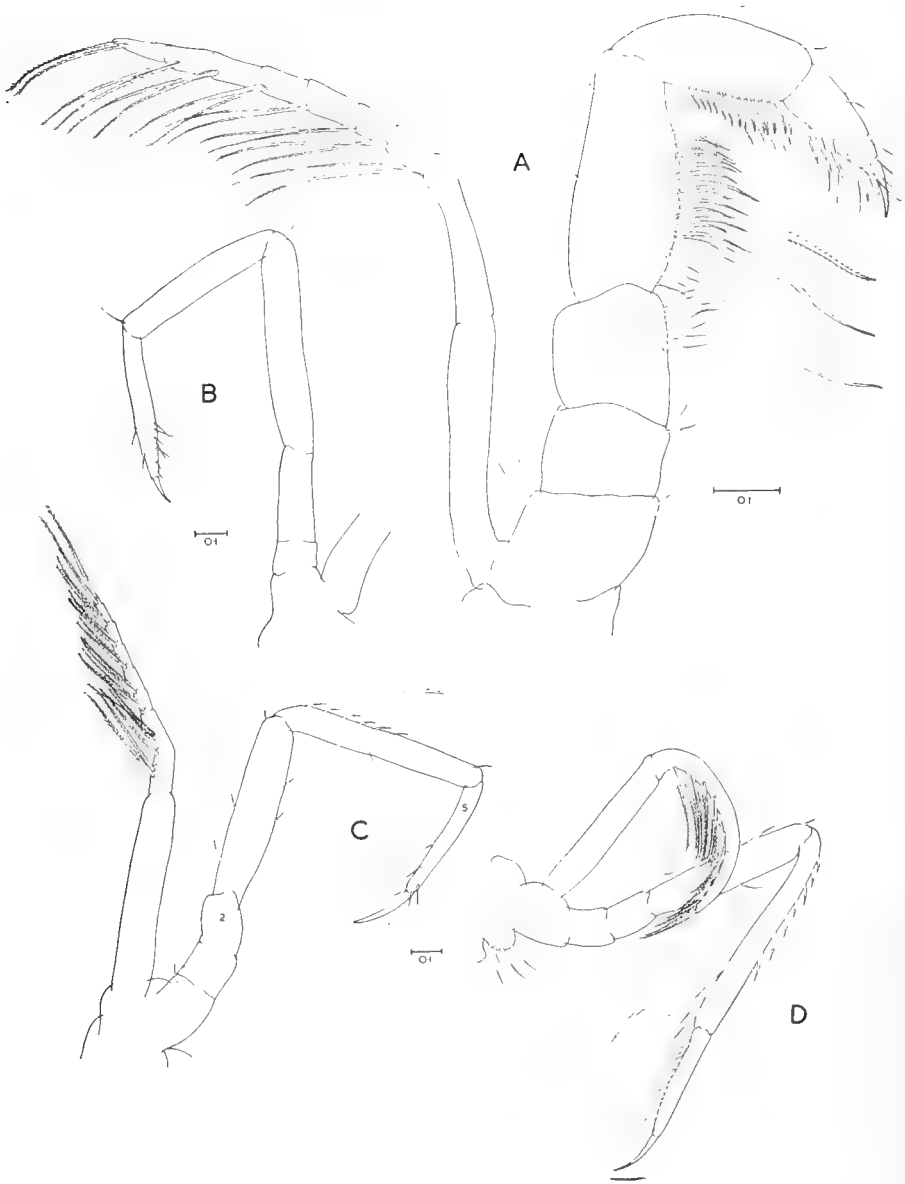


FIG. 3. *Spelaeomysis servatus* (Fage). Male, 5·5 mm, t.l. Aldabra Atoll. *A*. *B*. *C*. *D*. Second, fifth, seventh, eighth right thoracic limbs respectively, ventral aspects. Scales in mm.

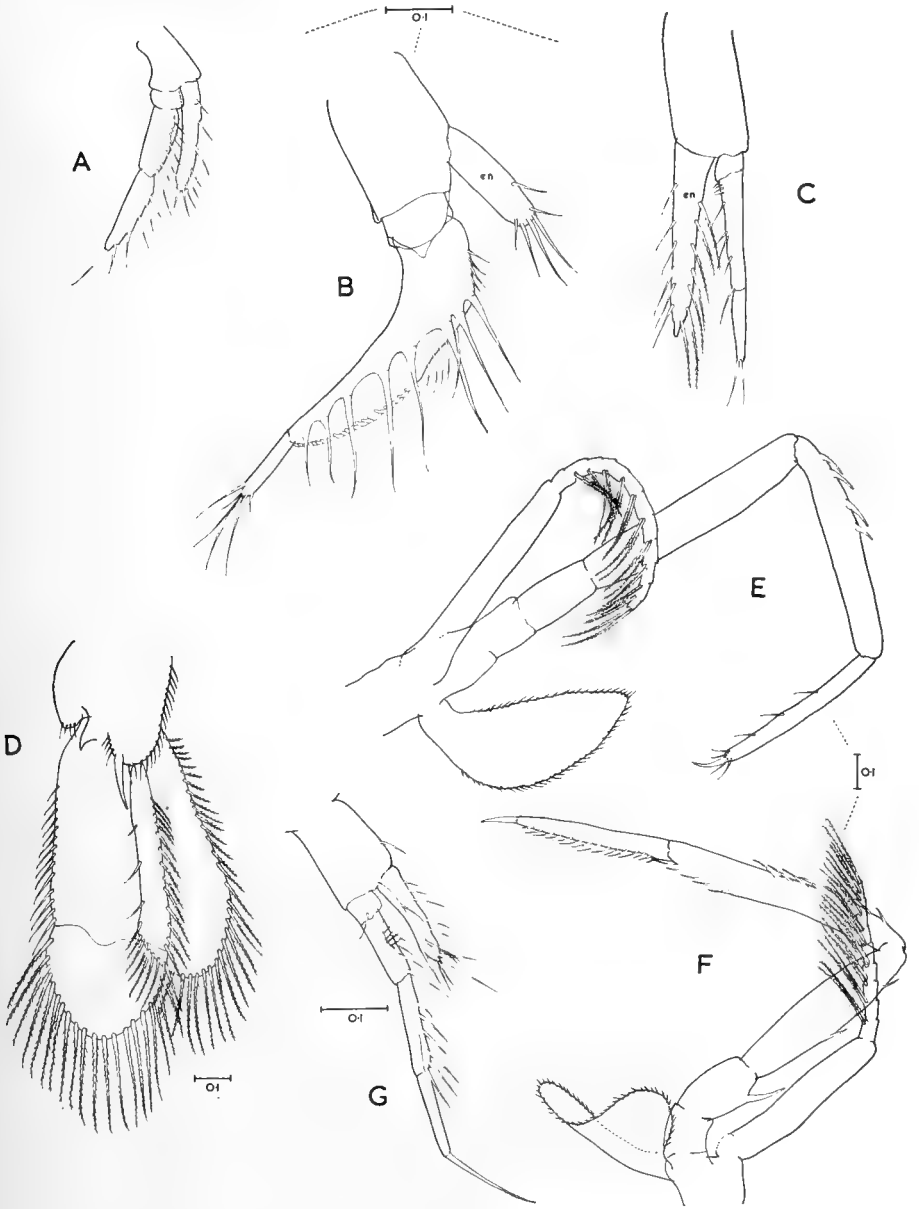


FIG. 4. *Spelaeomysis servatus* (Fage). Aldabra Atoll. Male 5·5 mm, t.l. *A*. *B*. *C*. First, second, third right pleopods respectively. *D*. Right uropod. Female 6 mm, t.l. *E*. *F*. Seventh and eighth thoracic limbs respectively. *G*. Second right pleopod. All ventral aspects. Scales in mm.

oblique sinuous ridge arising from ventral surface of second segment invested with long setae. Pleopods three (Fig. 4*C*) to five similar in shape. Uropods longer than telson, ventral distal margin of sympod prolonged backwards and shaped as depicted in fig. 4*D* and with a long curved spine. Inner margin with short setae. Exopod with distal transverse suture, endopod one-segmented. Outer exopod margin, proximal to suture, with a graded row of non-plumose setae, rest of exopod margin with plumose setae. Endopod outer and distal margins invested with plumose setae.

Female. The female differs from the male in the following features. (1) Second to eighth thoracic limbs each bear an oostegite arising from inner surface of coxa (figs. 4, *E,F*), and increasing in size posteriorly. (2) Seventh thoracic limb (fig. 4*E*), with first endopod segment much shorter than second, third segment slightly less than three times length of second, fourth slightly shorter than third and with outer proximal row of four prominent pectinate setae, fifth segment about three-quarters length of fourth, claw about one fifth length of fifth segment. (3) Eighth thoracic limb (fig. 4*F*), with first endopod segment shorter than second, third about two and a half times the length of second, fourth with eight pectinate setae on outer proximal margin and five pectinate setae on inner distal margin, (shorter than those of male), claw slightly less than a quarter length of fifth segment. (4) Second pleopod (fig. 4*G*), with a four-segmented exopod second segment shorter than either third or fourth, fourth invested with a long stout setae.

Juveniles. The smallest specimens (♂ 3 mm, ♀ 4 mm), have the proportions of the segments of thoracic limbs similar to those described for the adult male. In particular, the claws of thoracic limbs seven and eight are nearly half the length of segment five of these respective limbs. Compared with the adults, juveniles have about half the number of setae on the fourth segment of thoracic limbs seven and eight, and in juvenile females only half the adult number of setae are present on the fifth segment of limb eight. The telson spines of juveniles are longer. The median spine is more than one third the telson length, whilst in adults it is less than one third of the length.

Remarks. The specimens of *Spelaeomysis servatus* from Aldabra, the original descriptions of the species by Fage (1924, 1925), and four specimens (3 ♀♀ and 1 ♂) of the type series examined, all agree, except in the following features. (1) The eyestalks of the Aldabran specimens and of the four types are subquadrate, but do not have the inner distal margins acutely sloping as depicted by Fage (1925, fig. II). (2) The dorsal surfaces of segments two and three of the antennal sympod of the Aldabran and type specimens are not invested with setae as shown by Fage in his fig. III. (3) The structure of the male's second pleopod of the Aldabran material and of the type specimen examined does not agree with the figure of this appendage given by Fage in his fig. IV. This difference may be due to an abnormal flattening of his material after mounting as a micro-preparation. (4) Fage figures very short telson spines (his fig. VII), the median spines measuring only about one sixth of the telson length. These spines on the Aldabran and the type specimens examined measure about one third of the telson length.

Discussion. *Spelaeomysis servatus* was first collected in the surface lake water of a coralline grotto on Zanzibar Island, E. Africa (see Allaud & Jeannel, 1914: 381). The specimens from Aldabra Atoll are from a limestone seepage pool and were also collected near the surface of the water during a flowing tide (personal communication from Dr. K. G. McKenzie). Both habitats are similar and of the type in which members of the hypogean fauna are often found. Although the Aldabran specimens were taken from an exposed pool, it seems unlikely that this is their normal habitat. It is possible that they were carried into this surface pool by the upwelling of water caused by the incoming tide passing through the subterranean limestone interstices. Whether, on Aldabra, this mysid inhabits hypogean water that is cut off from the surrounding sea (and is of a lower salinity), or whether it is a true marine subterranean dweller, remains to be investigated. At present there is little information available about the biotopes of the other species of *Spelaeomysis*.

Gordon (1960 : 308) defined the family Lepidopidae (now Lepidomysidae). This family contains two genera at present, *Lepidomysis* Clarke, (1961) and *Spelaeomysis* Caroli, (1924). The genus *Spelaeomysis* was redefined by Pillai & Mariamma, (1964 : 223) and all the features listed in their definition, except for "eye-plates without visual elements", are present in material examined of *L. servatus*. The presence or absence of visual elements does not constitute a valid generic character, as in the Mysidacea these elements can be developed, reduced or can be absent in different species within the same genus (Pillai & Mariamma, 1964 : 119). There is no justification, therefore, for maintaininig two genera in the family Lepidomysidae, and the species *Lepidomysis servatus* is now transferred to the genus *Spelaeomysis* Caroli. This last generic name has precedence over *Lepidomysis* Clarke, 1961. The family Lepidomysidae and the genus *Spelaeomysis* can now be defined as follows: Body depressed or sub-cylindrical. Carapace produced antero-laterally into two rounded lobes and postero-laterally into large wings. Last two thoracic segments dorsally exposed, penultimate segment with anteriorly directed dorsal scale overlapping postero-median margin of carapace. Sixth abdominal segment slightly longer than fifth. Telson triangular or linguiform with margins partly or completely spinose. One or two eye-plates with or without visual elements. Labium with lobes well separated. Mandible with well developed incisor and molar processes; palp large and with robust pectinate spines on outer margin of second and third segments. Maxillule with a two-segmented reflexed palp bearing a long distal seta. Maxilla with inner margin of endopod segment expanded. Endopod of first thoracic limb with well developed endites, exopod reduced to a small unsegmented scale, epipod large. Endopod of second thoracic limb stout, exopod long and segmented. Thoracic limbs three to eight sub-equal or eighth very long. Coxa of eighth limb of male with penial lobe (?absent in *S. bottazzii*). Coxae of second to eighth thoracic limbs of female with oostegites. Pleopods alike in both sexes, except for sexual dimorphism of second pair, increasing in size from first to fifth pair, biramous, with one segmented-endopod and three-segmented exopod (four-segmented on second pair in female). Chitinous lamellae on postero-ventral margins of abdominal segments three to five. Uropod with a backward prolongation of sympod, exopod with a lateral suture (very faint in *S. bottazzii*), endopod without statocyst.

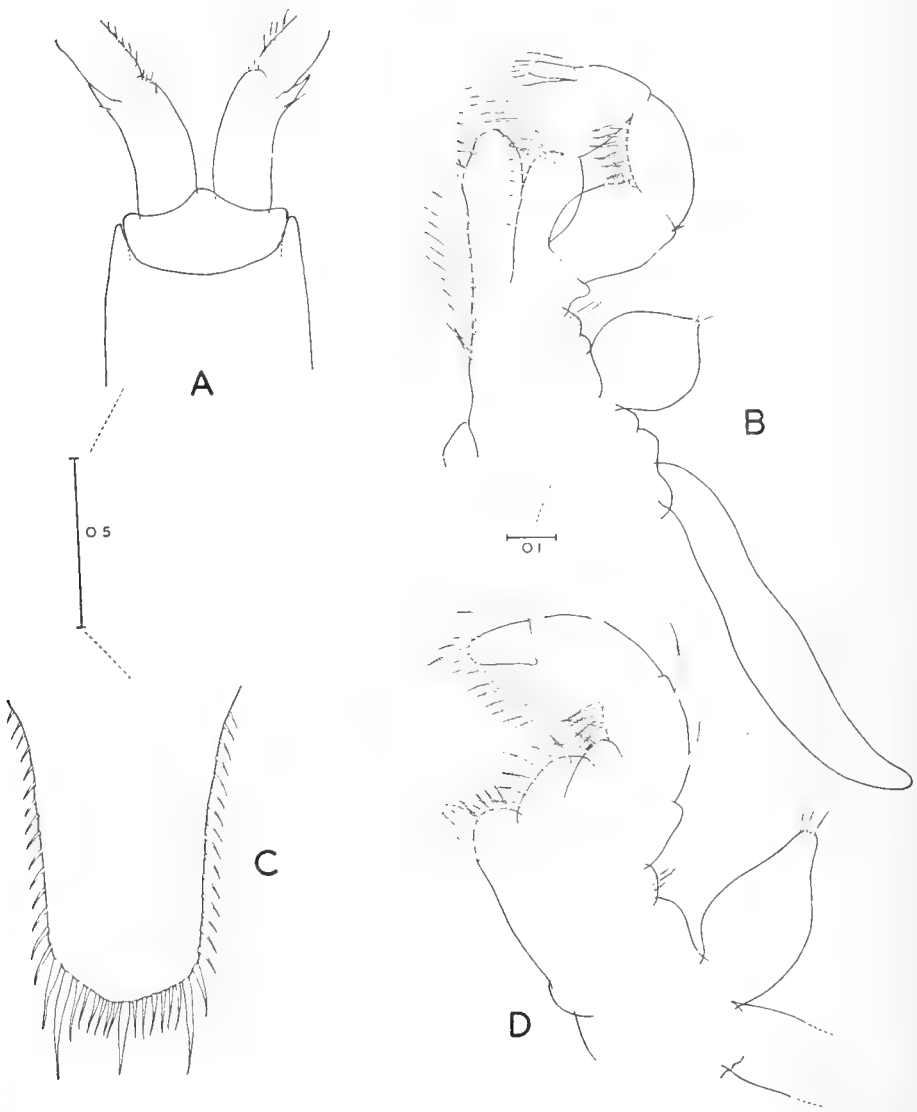


FIG. 5. *A*. *Spelaeomysis longipes* Pillai & Mariamma. Male, 5·6 mm, t.l. paratype, Kottayam, Kerala, India. Anterior portion of carapace, eye-plate and peduncular segments of antenna, dorsal aspect. *B*. *Spelaeomysis quinterensis* (Villalobos) male 7·5 mm, t.l. paratype, Gruta de Quintero, Mexico. First left thoracic limb, dorsal aspect. *Spelaeomysis bottazzii* Caroli, female 10·0 mm, t.l. Terra d'Otranto, Italy. *C*. Telson, dorsal aspect. *D*. First left thoracic limb, dorsal aspect. Scales in mm.

KEY TO DETERMINATION OF THE SPECIES OF THE GENUS *SPELAEOMYSIS* CAROLI

1 (2) A pair of eye-plates present (fig. 1*A*). Antennule, basal segment, outer distal margin not produced 3

2 (1) A single eye-plate present (fig. 5*A*). Antennule, basal segment, outer distal margin produced as a conical acute process (fig. 5*A*).
Spelaeomysis longipes Pillai & Mariamma (Kerala)

3 (4) First thoracic limb (fig. 2*E*), fifth segment (5) stout, length equal to or slightly exceeding breadth, inner margins of basis (b) and of endopod first segment expanded as broad endites 5

4 (3) First thoracic limb (fig. 5*B*), fifth segment slender, length greater than breadth, inner margins of basis and that of endopod first segment expanded as narrow endites . . . . ***Spelaeomysis quinterensis*** (Villalobos) (Yucatan)

5 (6) Distal two thirds of telson margin with spines, apex rounded (fig. 1*F*). Eye-plates with visual elements (fig. 1*A*). First thoracic limb (fig. 2*E*), fifth segment (5), length equal to breadth, fourth segment inner margin with strongly produced endite. ***Spelaeomysis servatus*** (Fage) (Zanzibar, Aldabra)

6 (5) Whole of telson margin with spines, apex sub-acute (fig. 5C). Eye-plates without visual elements. First thoracic limb, fifth segment, length exceeding breadth (fig. 5*D*), fourth segment with inner margin not strongly produced.
Spelaeomysis bottazzii Caroli (Otranto)

ACKNOWLEDGEMENTS

I must sincerely thank Dr. O. S. Tattersall for reading through the manuscript of this paper and for making available to me a part of Villalobos' paper translated into English. I am also grateful to Dr. K. G. McKenzie for providing information on the Aldabran habitat of *S. servatus*.

REFERENCES

ALLAUD, CH. & JEANNEL, R. 1914. In: R. Jeannel & E. G. Racovitza. Énumération des grottes visitées 1911–1913. *Archs Zool. exp. gén.* (Biospeologica XXXIII) **53** : 325–558.

CAROLI, E. 1924. Su di un misidaceo cavernicolo (*Spelaeomysis bottazzii* n.g., n.sp.,) di Terra d'Otranto. *Atti Accad. naz. Lincei Rc.* **33** : 512–513.

CLARKE, WM. D. 1961. Proposal of a new name, *Lepidomysis*, for the preoccupied mysidacean generic name *Lepidops* Zimmer, 1927. *Crustaceana* **2** : 251–252.

FAGE, L. 1924. Sur un type noveau de Mysidacé des souterraines de l'île de Zanzibar. *C.r. hebd. Seanc. Acad. Sci., Paris* **178** : 2127–2129.

—— 1925. *Lepidophthalmus servatus* Fage. Type noveau de Mysidacé des eaux souterraines de Zanzibar. *Archs Zool. exp. gén.* (Biospeologica LI) **63** : 525–532.

GORDON, I. 1960. On a *Stygiomysis* from the West Indies, with a note on *Spelaeogriphus* (Crustacea, Peracarida). *Bull. Br. Mus. nat. Hist.* (Zool.) **6** : 285–324.

McKenzie, K. G. 1971. Entomostraca of Aldabra, with special reference to the genus *Heterocypris* (Crustacea, Ostracoda). *Phil. Trans. R. Soc.* B **260** : 257–297

Pillai, N. K. & Mariamma, T. 1964. On a new Lepidomysid from India. *Crustaceana* **7** : 113–124.

Villalobos, A. 1951. Un nuevo misidaceo des las Grutas de Quintero en el Estado de Tamaulipas. *An. Inst. Biol. Univ. Méx.* **22** : 191–218.

Zimmer, C. 1927. Mysidacea. In: W. Kukenthal & T. Krumbach, Handbuch der Zoologie, **3** (1) : 607–750, (W. de Gruyter, Berlin, Leipzig).

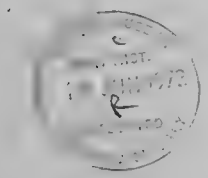
Dr. R. W. Ingle
Department of Zoology
British Museum (Natural History)
Cromwell Road
London, SW7 5BD

A LIST OF SUPPLEMENTS TO THE ZOOLOGICAL SERIES OF THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY)

1. KAY, E. ALISON. Marine Molluscs in the Cuming Collection British Museum (Natural History) described by William Harper Pease. Pp. 96; 14 Plates. 1965. (Out of Print.) £3.75.
2. WHITEHEAD, P. J. P. The Clupeoid Fishes described by Lacepede, Cuvier and Valenciennes. Pp. 180; 11 Plates, 15 Text-figures. 1967. £4.
3. TAYLOR, J. D., KENNEDY, W. J. & HALL, A. The Shell Structure and Mineralogy of the Bivalvia. Introduction. Nuculacea-Trigonacea. Pp. 125; 29 Plates, 77 Text-figures. 1969. £4.50.
4. HAYNES, J. R. Cardigan Bay recent Foraminifera (Cruises of the R.V. *Antur*) 1962–1964. (*In press.*)

Printed in England by Staples Printers Limited at their Kettering, Northants. establishment

RECENT RECORDS OF MAMMALS (OTHER THAN BATS) FROM ETHIOPIA



G. B. CORBET
AND
D. W. YALDEN

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 22 No. 8
LONDON : 1972

RECENT RECORDS OF MAMMALS (OTHER THAN BATS) FROM ETHIOPIA

BY

GORDON BARCLAY CORBET

AND

DEREK WILLIAM YALDEN

University of Manchester

BRITISH MUSEUM
NAT. HIST.
19 JUN 1972
PRESENTED
ZOOLOGY LIBRARY

Pp. 211-252; 3 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 22 No. 8
LONDON : 1972

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series, corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 22, *No.* 8 *of the Zoological series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation
Bull. Br. Mus. nat. Hist. (Zool.).

© Trustees of the British Museum (Natural History), 1972

TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 14 *June* 1972 *Price* £1.55

RECENT RECORDS OF MAMMALS (OTHER THAN BATS) FROM ETHIOPIA

By G. B. CORBET & D. W. YALDEN

CONTENTS

	Page
SYNOPSIS	213
INTRODUCTION	213
COLLECTING LOCALITIES	
The 1964 (Royal Military Academy) Expedition	214
The 1966 (Royal Military Academy) Expedition	216
The 1968 (Great Abbai) Expedition	216
The Wellcome Parasitology Unit	222
SYSTEMATIC LIST	
Insectivora	223
Primates	225
Lagomorpha	226
Rodentia	227
Carnivora	239
Hyracoidea	241
Tubulidentata	242
Perissodactyla	242
Artiodactyla	242
DISCUSSION	245
ACKNOWLEDGEMENTS	249
GAZETTEER	249
REFERENCES	250

SYNOPSIS

Recent expeditions to Ethiopia collected about 400 mammal specimens for the British Museum (Natural History), and these are identified and discussed. Four species are apparently new to Ethiopia, the shrews *Crocidura niobe* and *Suncus etruscus*, the murid *Arvicanthis somalicus*, and the cane rat *Thryonomys gregorianus*. In addition, there are several species that have been reported from Ethiopia only rarely, including *Tachyoryctes macrocephalus*, *Taterillus emini*, *Lemniscomys striatus*, *Praomys fumatus* and *Proteles cristatus*.

The peculiar zoogeographic relationships of the Ethiopian (i.e. Abyssinian) fauna are discussed in the light of these and previously published records. While an exhaustive examination of the mammalian fauna is not yet possible, it is evident that parallels exist with the better known avian and lepidopteran faunas.

INTRODUCTION

THE mammals of Ethiopia are relatively poorly known, and there has never been any comprehensive published account. Many East African species were first described from Ethiopian material, e.g. by Cretzschmar (1826) and Heuglin (1877), but these collections came mainly from the coast of the Red Sea. The main collections from Ethiopia in the British Museum are those made by P. Zaphiro in 1905, especially in

the southern half of the country, and by Major R. E. Cheesman about 1926 to 1932, mainly in the central highlands, but neither of these were reported upon except to describe individual novelties, e.g. by Thomas (1928). De Beaux (1925, 1943) added further records, and recently Ingersol (1968) has collected the mammals of the Harar area. Blower (1968) has given a more general account of the wildlife of Ethiopia.

In 1964 and 1966, adventure training expeditions from the Royal Military Academy, Sandhurst, collected mammals for the British Museum, principally in the region around Lakes Shamo and Abbaya in the Great Rift Valley, south of Addis Ababa (Anon., 1965, 1967). In 1968, the Great Abbai Expedition collected further specimens, particularly along the valley of the Blue Nile (=Great Abbai), and also more widely in central Ethiopia (Anon., 1970; Blashford-Snell, 1970). It is this last collection that forms the main basis for this paper, but relevant information from the other collections is included. D.W.Y. was a member of the Great Abbai Expedition and is responsible for the reports of field observations. G.B.C. identified the collection and supplied the taxonomic notes.

The Chiroptera are not included here, as they have been considered separately by Hill and Morris (1971).

COLLECTING LOCALITIES

Localities in Ethiopia are frequently difficult to trace, sometimes because of changes of name, but also due to the phonetic rendering of native names in different European languages (English, French, German and Italian, at least). The main localities (and alternative names) are therefore given here with geographical co-ordinates, altitude, and the dates of collecting at each. The co-ordinates were taken from the 1 : 100000 scale world maps, series GSGS 4646, sheets NC36, 37 and 38, although in some instances there were apparent discrepancies between these maps and astrofixes taken in 1968. In the absence of a botanist on the expeditions, ecological notes are necessarily vague. Since some of the localities, at least, have been little investigated, it has seemed worthwhile to mention also the sight records of larger mammals.

The 1964 (Royal Military Academy) Expedition

The 1964 Sandhurst expedition collected about 40 mammals from two areas, one in the region of the Rift Valley Lakes, the other further north near Lake Tana.

Soddu, 6° 45′N, 37° 40′E, altitude 1500 m. Collecting here extended from 8–23 August 1964, and was carried out in the area south of Soddu toward the north shore of Lake Abbaya—specimens are referred in the taxonomic list to Soddu, in order to distinguish them from material collected in 1966. This area is in the rift valley and is rather dry, with some cultivated patches but much thick thorn scrub, isolated trees, and some rocky outcrops.

Little Abbai, 11° 20′N, 37° 00′E, altitude 2000 m. Collecting in the valley of the Little Abbai extended from 27th August to 5th September 1964. This area is on the main Ethiopian plateau, between the towns of Danghila and Bahar Dar, and

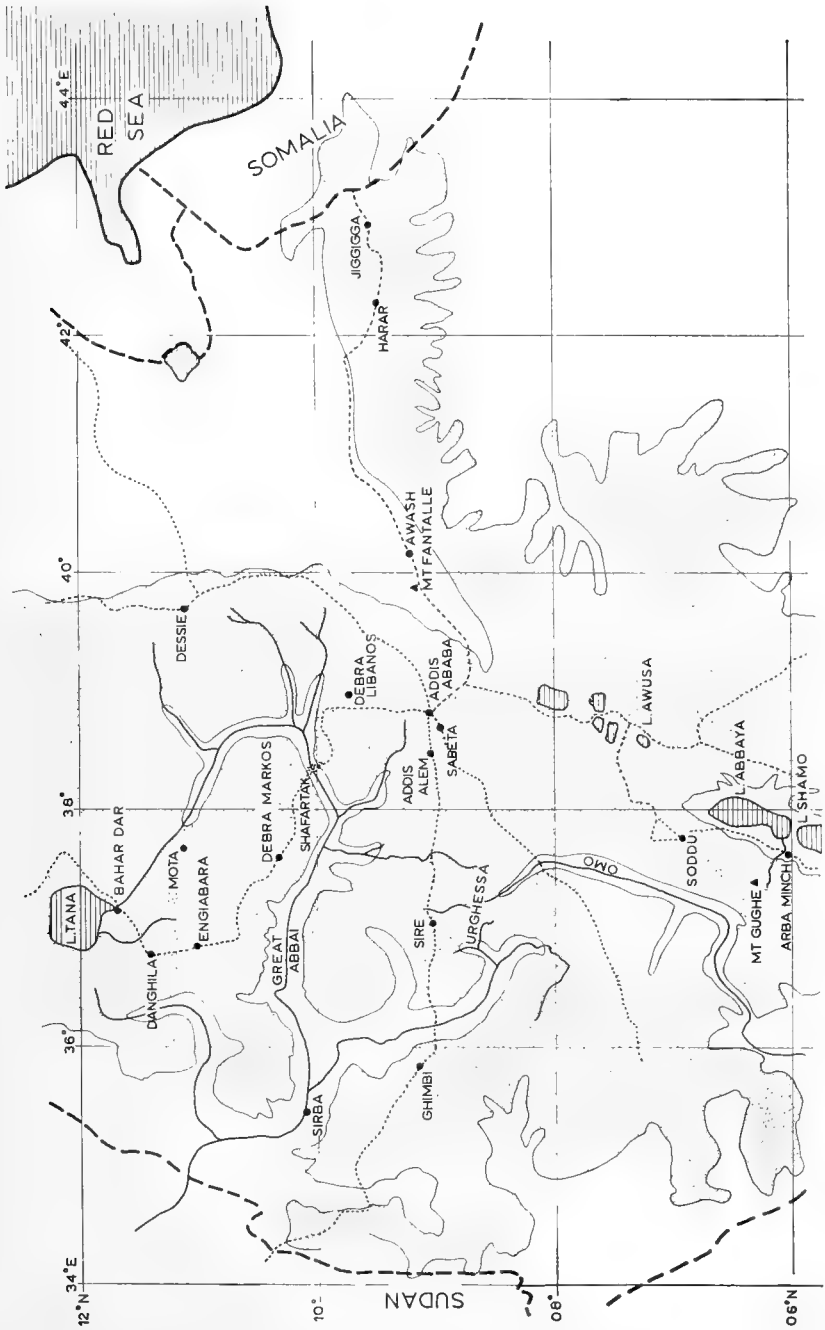


FIG. 1. Map of Ethiopia showing principal collecting localities. Ground over 1500 m is shaded.

south of Lake Tana. With the higher rainfall, rather more of the land is cultivated but there are also patches of scrub and some rocky outcrops.

The 1966 (Royal Military Academy) Expedition

The 1966 Sandhurst expedition collected about 90 mammals under the direction of Dr P. A. Morris from the Rift Valley Lakes region between 6th August and 3rd September 1966.

Lake Abbaya

Base camp was established at the S.W. corner of Lake Abbaya (=L. Margherita) near **Collufu River** at 6° 04′N, 37° 40′E, altitude 1500 m. **Arba Minch**, the provincial capital of Gemu Gofa, is 10 km west of the base camp site. There are small areas of cultivated land, but the dominant vegetation is thorn scrub. At the time of collecting, the area was extremely dry and dusty until the very end of the period when the rainy season began.

Darsi River flows into Lake Abbaya about 12 km north of the base camp. The lake shore region is very swampy, particularly at the mouth of the Darsi, and some collecting was carried out in this region.

Some collecting was also carried out in the **Bonchie** (Bonghe) Valley, 6° 05′N, 37° 20′E, some 35 km west of the base camp, on the lower slopes of **Mount Gughe**, at about 2700 m. This is an area of riverine forest, with closed canopy, plentiful creepers, and sparse, though lush, ground cover, but with some cultivation.

Lake Shamo

Lake Shamo (=Chamo, Ciamo; also =L. Ruspoli) lies immediately south of Lake Abbaya in the Rift Valley. Some collecting was carried out in an area known colloquially as the 'White Grasses', east of the isthmus between the two lakes, at 5° 58′N, 37° 55′E, at an altitude of 1500 m. This is the area shown on the map by Blower (1968) as the proposed Lake Chand (a misprint for Chamo?) Game Reserve. It is an extensive rolling plain with stony soil and dry, white, grass sharply delimited from the surrounding thorn scrub and hillsides. Sight records here included herds or spot counts of 96 common zebra, *Equus burchelli boehmi*, 16+ waterbuck, *Kobus defassa*, 46+ Grant's gazelle, *Gazella granti*, 104 hartebeest, *Alcelaphus buselaphus swaynei* and 9+ warthog, *Phacochoerus aethiopicus*. The herd of *A.b. swaynei* is believed to be the largest herd known of this race which is on the verge of extinction (Simon, 1968).

The 1968 (Great Abbai) Expedition

This expedition was in the field during August and September 1968. The main object was a navigation of the Blue Nile (Great Abbai) from near its source at Lake Tana to a point near the border of Ethiopia and the Sudan. Most of the zoological collecting was therefore carried out in the Blue Nile Gorge, but specimens were also obtained near the various base camps established on the plateau, and elsewhere in Ethiopia.

The zoological team on the Great Abbai Expedition (Dr P. A. Morris, Dr M. J. Largen, Mr H. King and D.W.Y.) were responsible for most of the collecting including that in the Blue Nile Gorge, at Bahar Dar, Harar, and Awash. Collecting at Ghimbi, and much of that at Debra Markos, was undertaken by other members of the expedition. Most small mammals were collected with various types of break-back trap, of 'rat' and 'mouse' sizes, while a few were caught by hand or killed with dust shot. Larger mammals were shot at night. Hunting was unsuccessful in the Blue Nile Gorge, primarily because of the difficulty of moving about quietly on difficult terrain in the dark, but perhaps also due to a genuine scarcity of larger mammals. Elsewhere, such hunting was most productive. A general account of the progress and organization of the expedition is given by Blashford-Snell (1970), Snailham (1970) and Anon. (1970).

Debra Markos (Debre Markos)

The main base for the expedition was established beside the airfield at Debra Markos, the provincial capital of Gojjam, 10° 20'N, 37° 50'E, altitude 2500 m. Limited collecting was carried out here from 4–27 August 1968. This area is part of the main Ethiopian plateau, and is intensively farmed. Mostly the farmland is pasture for cattle and sheep, but there is also some arable farming. Very little native vegetation remains; the native trees have been replaced by introduced *Eucalyptus* sp., and there are no hedgerows, or even walls, between the fields, which are demarcated instead (if at all) by ditches. The airfield itself carried some low, overgrazed, *Acacia* scrub. No wild ungulates were seen, but spotted hyaenas, *Crocuta crocuta*, were common in and around the town. Two jackals, *Canis aureus*, were seen on the airstrip, and a burrow of aardvark, *Orycteropus afer*, was found. Among the rodents trapped in the area were *Arvicanthis niloticus*, *Lophuromys flavopunctatus*, *Mus mahomet* and *Otomys typus*.

A limited amount of collecting was also carried out along the main road which runs north-west from Debra Markos to Bahar Dar through **Engiabara** and **Danghila** (11° 15'N, 36° 55'E) and southeast to Shafartak Bridge through **Degen** (=Dejem, Gunghi) (10° 10'N, 38° 05'E). The whole of this stretch of road runs along the Ethiopian plateau at around 2500 m, through similar pastoral country.

Blue Nile Gorge

The main collections in the Blue Nile gorge were made during stops on the journey by river from Shafartak road bridge westwards for about 400 km to a point near Sirba. Within this stretch of the river, a series of 'forward bases' (F.B.1, F.B.2, F.B.3) were established and most collecting was done at these, but some specimens were obtained at other, temporary, stops.

Shafartak Bridge (Bridge of Gojjam) 10° 06'N, 38° 17'E, altitude 1150 m.

Guder River, junction with the Blue Nile, 9° 50'N, 37° 41'E, altitude 1000 m. This was the location of Forward Base One (F.B.1), 85 km west of Shafartak. Collections were made from 8–11 August 1968. The gorge in this area, known col-

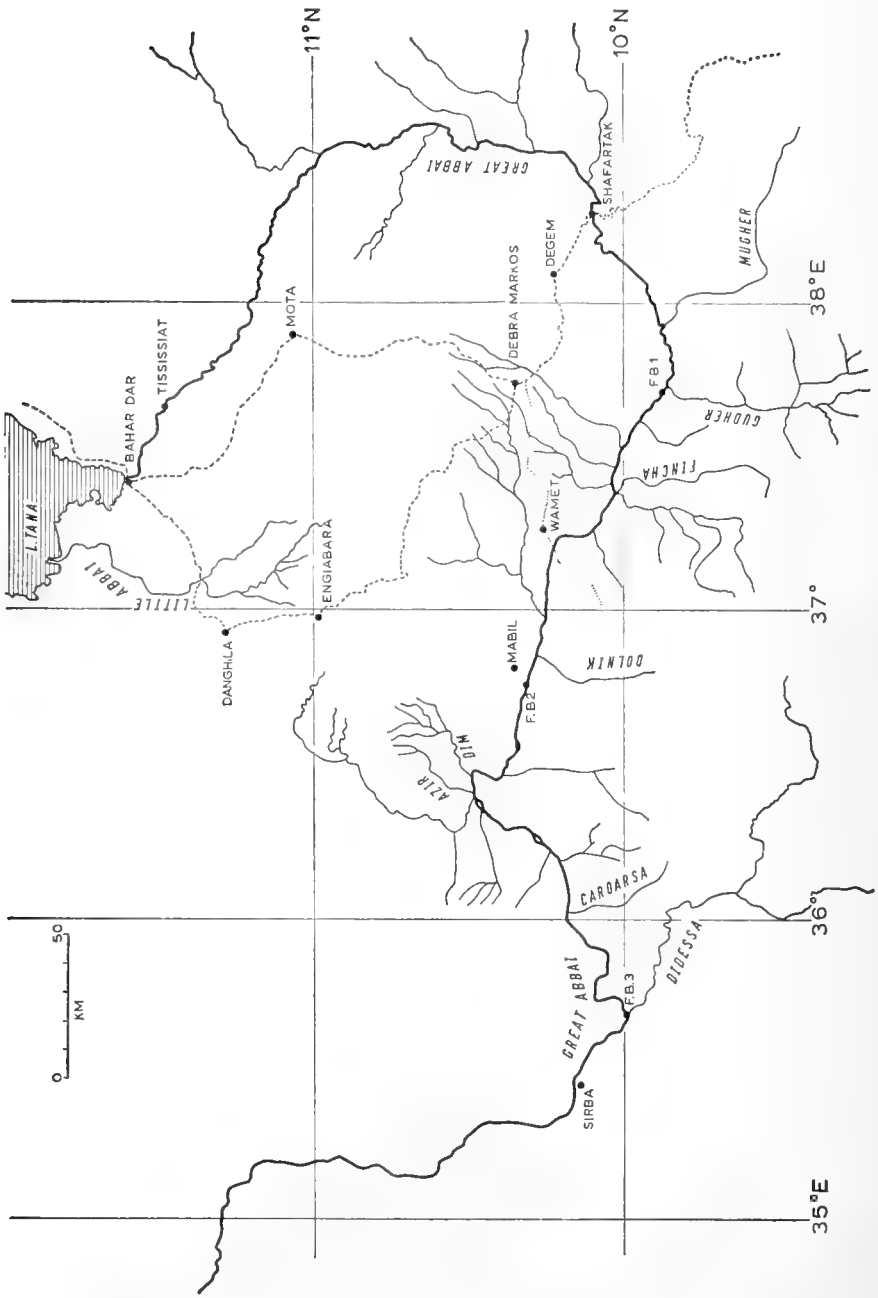


FIG. 2. Map of the Blue Nile showing localities studied during the Great Abbai Expedition.

loquially as the Black Gorge (Blashford-Snell, 1970), is extremely steep-sided, making progress either along or away from the river very difficult. The gorge is entirely uninhabited in this area, except for a Water Resources Board station about 2 km upstream on the Guder (whose flow it monitors). The vegetation consists of a small strip of riverine forest, only one to a few trees wide, and a dry semi-closed thorn scrub away from the rivers and water courses. At the time of collecting, the vegetation was all extremely green, but aerial reconnaissance during the previous dry season revealed a very difficult picture; then, there was only a thin strip of green riverine forest along the rivers, and brown vegetation behind, with the ground cover completely desiccated, and the thorn bushes leafless.

During the journey downstream from Shafartak to F.B.1, a single leopard, *Panthera pardus*, was seen beside the Blue Nile, and troops of olive baboons, *Papio anubis*, were seen, 6 km and 3 km east of the mouth of the Mugher River, 9° 50′N, 37° 55′E. Another troop was reported from the higher ground above F.B.1, and the villagers there also claimed that there was a group of six lions, *Panthera leo*, but this could not be confirmed. Within the gorge, in the immediate neighbourhood of the Forward Base, no trace of larger ungulates or carnivores were seen. Quills of porcupine, *Hystrix cristata*, were found in the area, and at the mouth of the Mugher River. The only small mammals caught were *Acomys* sp. and *Dendromus mystacalis*.

Fincha (=Fingiar) **River**, junction with the Blue Nile 10° 03′N, 37° 20′E, altitude 1000 m. This was a temporary base, where there was some collecting from 11–13 August 1968. The general terrain and vegetation were the same as F.B.1.

In moving from F.B.1 to the Fincha River on 11 August, two klipspringer, *Oreotragus oreotragus*, were seen on the cliffs, and tracks of *Papio anubis* were found on the river bank. A single *Colobus guereza* was seen in the riverside trees about 1 km west of F.B.1, and two warthog, *Phacochoerus aethiopicus*, were seen en route. At the mouth of the Fincha, quills of *Hystrix cristata* were again found, and at least two hyraxes, *Procavia habessinica* were seen. The only small mammal trapped here was the sole dormouse, *Graphiurus murinus*, obtained by the expedition.

Mabil. Forward Base Two was established on the bank of the Blue Nile at 10° 19′N, 36° 45′E, about 8 km S.W. of Mabil village, and 10 km W. of the Dolnik River at 900 m. Collecting here occupied 14–20 August 1968.

Travelling west from the Fincha to F.B.2, on the 14th August, the first 10 km of the journey continued through steep-sided gorge, and a further two klipspringer were seen. These were the last ones seen along the river, however, for further westwards the valley opens out. The vegetation remains essentially the same, with just a thin strip of tall trees and a deciduous thorn scrub hinterland. The valley remains uninhabited, but small patches of cultivated land (mostly with maize) suggest temporary, perhaps seasonal farming. With the river flowing more slowly, hippopotamus, *Hippopotamus amphibius*, were seen for the first time, two east and two west of the Wamet (Uamet) ford at 10° 09′N, 37° 12′E, and at least nine small troops of *Papio anubis*. Another single *Colobus* was noted 1 km west of Wamet.

Sight records at F.B.2 included single specimens of the mongoose, *Ichneumia albicauda* and a male bushbuck, *Tragelaphus scriptus*, while most of the small mammals caught were *Mus* sp., probably *Mus pasha* and *Mus tenellus*.

Azir River. A temporary base was established from 20–22 August 1968 near the Azir River at 10° 29′N, 36° 25′E, altitude 800 m. The Blue Nile from F.B.2 to the Azir River continues through the rather wider valley. A party of *Colobus* was seen at the mouth of the Dim River (10° 30′N, 36° 26′E) and there was another party in the vicinity of the temporary base. There were also small groups of vervet monkeys, *Cercopithecus aethiops*, at both these localities. A single warthog was seen at the base, and tracks were numerous, as were those of hippopotamus. A number of mice, *Praomys natalensis*, were trapped here.

Caroarsa River. A temporary base was established 10 km east of the Caroarsa River, at 10° 07′N, 36° 12′E, altitude 600 m. Collections date from 23–24 August. From the Azir River to some distance west of the Caroarsa, the sides of the Blue Nile Gorge close in to give a steep-sided rocky valley again, known colloquially as the Western Cataracts. However, the river is not so consistently turbulent as in the Black Gorge and a dozen hippopotamus were counted during the journey west to the Caroarsa on 22 August. There was a small party of *Cercopithecus aethiops* in the vicinity of the temporary base, and at least one, perhaps two, *Colobus*. Traces of porcupine and hyrax (?*Procavia habessinica*) were found, while there were tracks of leopard on the river bank. Ungulate tracks, possibly bushbuck, were also noted. Only three rodents were trapped, single specimens each of *Lemniscomys striatus*, *Mus tenellus* and *Acomys ?dimidiatus*. The vegetation at this locality was more lush than elsewhere, a deeper band of riverine forest stretching back for at least 100 m from both banks of the river. As indicative of the added moistness in the area, it was the only site along the Blue Nile from Shafartak westwards where mosquitoes were troublesome.

Didessa River. Forward Base Three was established on an island at the mouth of the Didessa River, 10° 05′N, 35° 38′E, altitude 450 m. Collecting extended from 26–29 August. The island and a thin strip along the river banks constituted a riverine forest, but up the valley sides this gave way as elsewhere to thin scrub. There was a flattish damp area with tall (over 2 m) grass penetrated by the trackways of hippopotamus, and inhabited also by what appeared to be cane rats, *Thryonomys* sp. From the Caroarsa westwards the Blue Nile runs in a widening valley and flows more gently. The first permanent habitations were noted in the Western Cataracts, and the valley became more densely populated, and more intensively cultivated, from there westwards. The nearest village to F.B.3 was about 5 km west, and there were maize fields on the opposite river bank. Small numbers of *Papio anubis*, *Colobus* and hippopotamus were recorded during the journey to the Didessa, and one or two hippopotamus were heard during the nights in the rivers beside F.B.3. A number of *Praomys natalensis* were caught in the native village nearby, while trapping in the river bank vegetation yielded several *Lemniscomys striatus*, *Crocidura ?sericea*, and *Acomys* sp.

Sirba, 10° 05′N, 35° 30′E, marked the western end of the journey downstream. No terrestrial mammals were collected there but four oribi, *Ourebia ourebi*, were seen on the mission airstrip at night on 30th August. The banks of the Blue Nile between the Didessa and Sirba are intensively cultivated, lacking anything more than the odd

remnant tree from the riverine forest, and no large mammals were seen during the last journey down river.

Ghimbi, Wollega Province

Ghimbi, 9° 10'N, 35° 50'E, altitude 2150 m, was a collecting area from 22–31 August 1968. Ghimbi is on the densely populated and intensively cultivated plateau, on the main road west from Addis Ababa. Some collecting was carried out in the town, and in the surrounding maize fields; other specimens came from rough bushland along the main road up to 30 km out of the town. Two specimens came from an area of savannah 24 km north of Ghimbi, at 9° 30'N, 35° 50'E, altitude 1600 m. The main rodents trapped here were *Rattus rattus* and *Lophuromys flavopunctatus*, while among carnivores shot here were *Felis serval, Ichneumia albicauda* and *Viverra civetta*. In addition specimens of *Orycteropus afer, Crocuta crocuta, Colobus guereza, Canis ?aureus* and *Phacochoerus aethiopicus* were reported seen in the area.

Bahar Dar, Gojjam Province

Bahar Dar (Bahr Dar, Bahadar) is located on the main road north from Addis Ababa to Gondar, at the point where it bridges the Blue Nile near the source of the river, 11° 35'N, 37° 25'E, altitude 1830 m. Although on the plateau this area is not so intensively farmed as the environs of Ghimbi and Debra Markos; moreover, there is little arable farming, perhaps because the ground is waterlogged in the wet season, or because the soil is shallow, and instead pastoral farming predominates. Numerous thickets and patches of thorn scrub remain, there is a thin strip of riverine forest along the Nile, and native tree species have not been replaced by the almost ubiquitous *Eucalyptus*. Collecting around Bahar Dar occupied 11–14 September 1968; it was concentrated in an area 15 km south-east of the town, along the road that follows the south bank of the Nile to the Tississiat Falls. Species seen in this area but not collected include *Cercopithecus aethiops, Papio anubis, Felis serval, Genetta* sp. and *Tragelaphus scriptus*. The principal rodent trapped was *Lophuromys flavopunctatus*, and specimens of the rodents *Praomys albipes, P. natalensis, Dasymys incomptus* and three species of crocidurine shrew were obtained.

Harar, Harar Province

Harar itself is on the high ridge that runs eastwards from the eastern wall of the rift valley, but collecting was carried out on the lower ground further east, along the road to Jiggigga. This area is rather sparsely populated, and is mostly very thin thorn scrub with little or no ground cover; some parts are very dry and rocky.

Bisidima River, 9° 15'N, 42° 12'E, altitude 1500 m. This locality was collected 20–21 September. There is some cultivation of maize, and collecting areas included the *Opuntia* hedges around these fields and rough thorn scrub. Trapping yielded specimens of *Rattus rattus, Praomys natalensis, Lophuromys flavopunctatus* and *Crocidura doriana*.

Valley of the Rocks, 9° 15'N, 42° 20'E, altitude 1300 m. An area of sparse *Acacia* woodland, with many boulders, cliffs and scree slopes, collected 21 September. Two klipspringer, *Orcotragus oreotragus*, were seen here, and *Procavia* was collected.

60 km East of Harar, 9° 14'N, 42° 32'E, altitude 1200 m. This is a sparsely inhabited area of thin *Acacia* scrub and very little ground cover, which was studied 21–22 September. Among mammals seen in this area were *Felis silvestris*, *Canis ?aureus*, *Ichneumia albicauda*, and a large troop of sacred baboons, *Papio hamadryas*. The only small mammals caught here were a gerbil *Taterillus ?emini* and a rat *Praomys fumatus*.

Awash, Shoa Province

Awash (=Auasc, Aouche) is well known as a National Park. It lies in the Great Rift Valley in an extension northwards of the more familiar East African *Acacia* savanna, mostly grass with scattered trees and bushes. There is a strip of riverine forest along the Awash River. The area is still moderately active volcanically, with recent lava flows and lava bubble caves, and is dominated by the quiet cone of Mount Fantalle which rises to 2000 m.

The lava bubble caves are of particular importance in the present context. Some of the lava bubbles have opened at the sides, to give normal caves which were used by bats and porcupines; others have collapsed in the top to form pitfall traps, and two of these, at 8° 56'N, 39° 57'E, yielded more than a hundred skulls of various animals.

Most collecting was carried out on the north bank of the Awash River at 8° 50'N, 40° 01'E, and a few specimens came from the area of the hot springs at Filhoa, 9° 00'N, 39° 58'E. Collecting lasted from 23–28 September 1968.

Naturally, in such a rich area for game sight records of many species were obtained. The principal ungulates were oryx, *Oryx gazella beisa*, and Soemmerring's gazelle, *Gazella soemmerringi*. Smaller numbers of waterbuck, *Kobus defassa*, lesser kudu, *Tragelaphus imberbis*, greater kudu, *T. strepsiceros*, and warthog, *Phacochoerus aethiopicus*, were seen, together with three gerenuk, *Litocranius walleri*. An aardvark was killed on the road in the Park; two leopards and two lions were seen, and a single hippopotamus occasionally wandered through the camp at night. A small troop of *Papio anubis* was seen frequenting the riverine forest along the Awash River, and small numbers of *P. hamadryas* were seen in the drier hinterland of the Park. A single zorilla, *Ictonyx striatus*, seen at night was the first record of that species in the locality. The principal small mammals caught were the gerbils *Taterillus ?emini*, *Gerbillus ?harwoodi* and *Tatera robusta*, spiny mice, *Acomys dimidiatus mullah*, and the shrew *Crocidura ?sericea*.

Wellcome Parasitology Unit

In addition to these collections, a number of specimens recently collected by the Wellcome Parasitology Unit based in Addis Ababa have been included. These came from the following localities.

Dessie (Dese), Welu Province, 10° 08'N, 39° 43'E, altitude 2700 m.

Sabeta, Shoa Province, 8° 55′N, 38° 40′E, altitude 2500 m.
Addis Alem, Shoa Province, 9° 03′N, 38° 25′E, altitude 2400 m.

SYSTEMATIC LIST

The taxonomy of most groups of the smaller mammals of Africa is in a very provisional state, especially at the level of delimiting the species. These problems can be solved only by comprehensive revision of each genus on a continental scale, which is out of place in a regional list such as this.

The following list is based primarily upon the collection made by the Great Abbai Expedition in 1968, but it also includes mention of all specimens collected by the expeditions from the Royal Military Academy in 1964 and 1966 and some other Ethiopian specimens recently received at the British Museum.

Identification has been attempted at the subspecific level only where the subspecies seem clearly defined or, more often, where the specimens can be confidently allocated to a form named from Ethiopia whose specific relationship is doubtful.

Order INSECTIVORA

Family **MACROSCELIDIDAE**—Elephant shrews

Elephantulus rufescens (Peters)

Lake Abbaya: one collected at Cullufu River, between Lake Abbaya and Lake Chamo.

This represents the north-western extremity of the range of *E. rufescens*, which is otherwise known in Ethiopia only from the southern border (Mega, Farda Robo, Murri) and from the Harar district, and extends south in the drier, short-grass steppes to Tanzania (Corbet & Hanks, 1968). This specimen differs from all other forms of *E. rufescens* in being very grey, with the mid-dorsal line very dark and the post-ocular spots and upper surface of tail almost black.

Family **SORICIDAE**—Shrews

Suncus etruscus (Savi)

Bahar Dar: one caught by hand under a stone in wet grassland.

This appears to be the first record of this minute shrew (or any pygmy *Suncus*) from Ethiopia. It is an adult male with the following dimensions: head and body 49 mm; tail 29 mm; hind feet 7 mm; condylo-incisive length 12·6 mm (13·2–13·7 mm in sample of 13 other *S. etruscus*); upper tooth row 5·3 mm (5·3—5·8 mm in 20 others); width across M^2—M^2 3·4 mm (3·6–4·0 mm in 22 others). It resembles the Mediterranean *S. etruscus*, and differs from the East African *S. infinitesimus* (Heller), in having the braincase exceedingly flat, with a depth of only 2·4 mm at the basisphenoid.

The only other records of *S. etruscus* from south of the Sahara appear to be one from northern Nigeria in the British Museum collection, reported by Morrison-Scott (1946), and one from Guinea (Heim de Balsac & Lamotte, 1957). The Nigerian

skull also has a short tooth-row (5·3 mm), but the rostrum is wider (M^2–M^2 3·8 mm) and the length of the skull is not determinable. The Ethiopian and Nigerian specimens differ from most available specimens from the main part of the species' range around the Mediterranean in the large size of the fourth unicuspid teeth and the lack of a concavity on the anterior margin of the large upper premolar, but both have the very flat skull of *S. etruscus*, and there seem to be no grounds for the view of Petter & Chippaux (1962) that the Nigerian one should be referred to *S. infinitesimus*.

Crocidura doriana Dobson

Bahar Dar: two trapped in thicket in wet grassland.

Debra Markos: two trapped in grazed *Acacia* scrub.

Harar: one from Bisidima River.

Awash: several skulls from the lava caves.

The two from Debra Markos are very large, exceeding any other specimens from Ethiopia available in the collection of the British Museum: upper tooth-rows 14·7 and 14·8 mm, condylobasal lengths 32·2 and 32·4 mm. The maxima for other Ethiopian skulls are 14·2 mm (n = 17) and 31·8 mm (n = 11) respectively, and Osgood (1936) gave 13·8 mm as the maximum length of upper tooth-row in 28 skulls from Ethiopia.

It is probable that this form should be treated as a race of *C. occidentalis* (Pucheron) or, with *occidentalis*, as a race of *C. flavescens* (I. Geoffroy).

Crocidura cf. ***sericea*** Sundevall

Awash: eight collected, possibly of this species; a further 42 damaged skulls were collected from the lava caves.

Blue Nile Gorge: two from the mouth of the Didessa River.

These are medium-sized shrews with a pale grey ventral pelage. Measurements of upper tooth-row of all the Awash skulls, totalling 49, give a unimodal distribution with a mean length of 9·02 mm (S.D. ± 0·37, range 8·0–10·1). These all show good agreement with specimens from Sudan that have been named *C. sericea*, and with the types of *C. hindei* Thomas (Kenya) and *C. h. marrensis* Thomas & Hinton (Jebel Marra, Sudan). Setzer (1956) allocated larger specimens from central Sudan to *C. s. sericea* and treated the smaller *marrensis* and *C. lutrella* Heller (from Lado Enclave) as races. The Ethiopian specimens agree more closely in size with *lutrella* and *marrensis* than with the specimens allocated by Setzer to *C. s. sericea* which had upper tooth-rows of 10·3 and 10·6 mm.

Crocidura niobe Thomas

Ilubabor Province: one collected by Drs Largen, Morris and Yalden east of Abiu (west of Gore), at 1500 m in forest in January 1971.

This species of shrew was apparently known only from the east side of Ruwenzori, Uganda between 2000 and 2500 m (Thomas, 1906), although it is possible that other

forms from the Congo and from West Africa may be conspecific. This locality is on the south-western edge of the Ethiopian plateau.

It is very dark greyish brown above and below, and the feet and tail are also dark. The tail is extremely slender, about 80% of the length of head and body, and has very sparse vibrissae on the proximal half only. Measurements are: head and body 70; tail 55; hind feet (without claws) 12; ear 9; condylobasal length 19·5; upper tooth-row 8·9.

Crocidura bicolor Bocage

Little Abbai: one collected.

Bahar Dar: one caught under a stone in wet grassland with thickets.

This is a small shrew with very dark greyish brown dorsal pelage and moderately dark grey ventral pelage. There is a further specimen in the British Museum from '140 miles S. of Addis Ababa' and Osgood (1936) recorded specimens (as *C. b. nana* Dobson) from Hadama on the Awash River and from Addis Ababa.

Order PRIMATES

Family **LORISIDAE**

Galago senegalensis E. Geoffroy—Lesser bush-baby

Ghimbi: one collected 5 km east of the town on the edge of cultivation.

Lake Chamo: two collected on north side of lake.

Family **CERCOPITHECIDAE**

Cercopithecus aethiops (L.)—Vervet monkey

Soddu: three collected.

Little Abbai: one collected.

Lake Abbaya: eight collected.

Blue Nile Gorge: small parties of six to eight seen at the Azir, Dim and Caroarsa river mouths, in or near riverine forest.

Bahar Dar: a party of about six seen in riverine forest.

Colobus guereza Rüppell—Black and white colobus

Soddu: one collected.

Little Abbai: one collected.

Blue Nile Gorge: fairly widespread, with sightings from practically the whole length of the river from the Guder westwards to the Didessa, involving about 20 animals altogether.

Papio anubis (Fischer)—Olive baboon

Lake Abbaya: one collected near Soddu, and two from Arba Minch.

Blue Nile Gorge: seen along the whole length of the river, except perhaps in the Black Gorge, in groups of up to 20.

Bahar Dar: a troop of nine seen on two occasions beside the road to Tississiat.

Awash: a small troop seen in the gallery forest along the Awash River, and reported to raid the camp site occasionally.

Papio hamadryas (L.)—Sacred baboon

Harar: a troop of about 120 seen crossing the Jiggigga road about 60 km east of Harar.

Awash: a small troop on the lower northern slopes of Mount Fantalle.

The ecological and ethological relationship between *P. hamadryas* and *P. anubis* in the Awash area has been studied by Kummer et al. (1970) who reported a zone of hybridization about 15–20 km wide. This, however, is narrow in relation to the mobility of these animals and suggests a considerable degree of reproductive isolation that justifies the retention of species rank for these two forms. There is an ecological separation of the two species, with *P. hamadryas* in the drier regions away from the river. Kummer (1968) has suggested that the juxtaposition of the two species is fairly recent, due to an eastward extension of the range of *P. anubis*.

Theropithecus gelada (Rüppell)—Gelada baboon

Debra Libanos, Shoa: the small colony here is a well known tourist attraction, and lives on cliff-tops not far from the main road north from Addis Ababa. These animals were seen on several occasions, but were the only ones observed.

Order LAGOMORPHA

Family **LEPORIDAE**

Lepus habessinicus Hemprich & Ehrenberg—Abyssinian hare

Harar: ♀ collected at Bisidima River; ♂ and ♀ collected 60 km east of Harar on Jiggigga Road.

Awash: ♂ and ♀ collected.

Lake Abbaya: ♀ collected near Soddu northwest of lake.

These specimens agree with *L. habessinicus* as recognized by Petter (1963), rather than his *L. capensis starcki*, in having only narrow margins of black outside the tips of the ears and in having deep, cement-filled grooves in the upper incisors. This species is closely related to *L. capensis*, if indeed it is distinct at all, and it differs from *L. whytei* (below) in the very soft pelage, longer ears, black and white tail and in having the anterior faces of the upper incisors in the same (transverse) plane.

Lepus ?whytei fagani Thomas—Bush hare

Bahar Dar: four collected in wet grassland with scattered thickets (two of them pregnant with one and two foetuses).

Ghimbi: three collected in bush country close to cultivation.

These specimens agree closely with the type of *fagani* (from Lake Tana). This form was at first allocated to '*L. crawshayi*' by Petter (1959) but later to *L. habessinicus* (Petter, 1963, 1967). The type of *fagani* seems clearly referable to the East African group commonly called *L. crawshayi* rather than to the *capensis* group to which *habessinicus* belongs; it and the specimens in the present collection have harsher pelage, brown on the sides of the tail, short ears, and upper incisors with oblique anterior faces.

However, the type of *crawshayi* de Winton (from central Kenya) seems to belong to the *capensis* group, and the earliest name for what Petter called *L. crawshayi* is probably *L. whytei* Thomas, 1894 from Malawi. Throughout East Africa *L. whytei* seems to be the short-eared, harsh-furred bush hare, whilst *L. capensis* is the long-eared, soft-furred species of the more open plains. All the present specimens of *L. habessinicus* are from the lower, drier areas in the south and east while the *L. ?whytei* all came from the plateau.

Order RODENTIA

Family **SCIURIDAE**—Squirrels

Heliosciurus gambianus multicolor (Rüppell)—Sun squirrel

Blue Nile Gorge: one collected at Mabil.

This squirrel seems identical to a large series in the British Museum from the upper part of the Blue Nile just below Lake Tana, whence it has also been reported by de Beaux (1925). These are lighter than two from Kaffa, presumably referable to *H. g. kaffensis* Neumann. The species does not appear to have been recorded on the Sudanese part of the Blue Nile.

Xerus erythropus leucoumbrinus (Rüppell)—Striped ground squirrel

Lake Abbaya: two from Soddu; one from Arba Minch.

Lake Chamo: one from northwest of the lake.

These localities are probably close to the northeastern limit of this species, the unstriped *X. rutilus* alone being found in the more eastern parts of the country.

Xerus rutilus (Cretzschmar)—Unstriped ground squirrel

Harar: Valley of the Rocks, 40 km east of Harar. At least three unstriped ground squirrels were seen in a rocky area of open *Acacia* woodland. They are presumably referable to this species, which was recorded from this area by Ingersol (1968).

Family **CRICETIDAE**

Subfamily **GERBILLINAE**—Gerbils

Gerbillus (Dipodillus) ?harwoodi Thomas

Awash: seven trapped in various parts of the region; a number of cranial fragments, probably of this same species, were found in each of the lava caves examined.

These small gerbils show good agreement with the type of *harwoodi* (from Naivasha, Kenya), but this must be treated as provisional pending a much-needed revision of this group.

Tatera robusta (Cretzschmar)

Awash: one trapped on north bank of river; a large number of skulls, probably of this species, from the two lava caves.

The greyish dorsal pelage of the only available skin gives this gerbil a closer resemblance to Sudanese *T. r. robusta* than to the more yellowish Somalian forms such as *shoana* and *phillipsi*. Setzer (1956) used the subspecific name *taylori* Hatt (Red Sea coast) for this species in eastern Sudan, but the skin from Awash differs from *taylori* and resembles *robusta* in having the dorsal hair of the tail black rather than brown.

Tatera valida soror Allen

Blue Nile Gorge: one from 10 km west of Mabil; one from the mouth of the Didessa River; mandibles, probably of the same species, from a cave at the mouth of the Guder River.

These agree well with the description of *soror*, from Fazogli on the Sudanese Blue Nile, which was allocated to *T. valida* by Davies (1968), although this must be considered tentative.

Taterillus ?emini (Thomas)

Harar: one from 60 km east of Harar on the Jiggigga road.

Awash: two from the north bank of the Awash River.

Both of these gerbils were in very dry, open *Acacia* scrub, the one at Harar close to maize cultivation, those at Awash close to riverside woodland.

There are no previous examples of this genus from Ethiopia in the British Museum except for the much smaller *T. harringtoni* from the Kenya border near Lake Rudolph. The specimens from Harar and Awash are richly coloured, with almost no grey showing in the pelage. They resemble *T. emini* from Sudan and Uganda in size, but differ in the posterior palatal vacuities which are unusually short for any *Taterillus*. Measurements are as follows (Harar followed by Awash): head and body 117, 119; tail (from pelvis) 127, 167; hind foot (without claw) 31, 32; ear 19, 16; condylobasal length 31·1, 33·7; upper molar row 4·9, 4·8; posterior palatal vacuities 3·0. 3·1.

Family **MURIDAE**

Genus ***ACOMYS***—Spiny mice

Acomys ?cahirinus (Desmarest)

Blue Nile Gorge: two from mouth of Guder River, trapped on a rocky hillside in thick bush.

Lake Abbaya: one from N.E. of Lake Chamo.

See remarks under *A. ?dimidiatus* below.

Acomys ?dimidiatus (Cretzschmar)

Blue Nile Gorge: one 10 km east of Caroarsa River, in riverine forest; three at mouth of Didessa River, in riverine forest and long grass.

Awash: four trapped in dry open *Acacia* scrub close to riverine woodland; remains of two animals from one of the lava caves.

The taxonomy of the spiny mice of the genus *Acomys* in this region is very provisional. The Awash animals agree very closely with the type of *mullah* Thomas from Harar, which Setzer (1968) referred to *A. dimidiatus*. These have large skulls, the only one with moderately worn teeth having a condylobasal length of 28·2 mm and with upper tooth-rows of 4·5, 4·5 and 4·6 mm.

The *Acomys* from the Blue Nile appear to fall into two groups. Two from the mouth of the Guder River are smaller, with upper molar rows of 4·1 and 4·3 mm and condylobasal lengths of 25·8 and 25·5 mm (both are adults with well worn teeth). The remaining four (Caroarsa and Didessa Rivers) have upper molar rows of 4·6, 4·8, 4·8 and 4·9 mm and the two with worn teeth have condylobasal lengths of 27·7 and 28·4 mm. Skins of these two groups are not distinguishable. The difference in size strongly suggests the presence of two species, but in the absence of both at the same locality and in more adequate numbers this cannot be considered certain. The smaller one is tentatively referred to *A. cahirinus* and agrees well, in size and in colour, with *A.c. cineraceus* Fitzinger & Heuglin from eastern Sudan to which Setzer (1956) referred animals from the Sudanese Blue Nile. If Setzer (1968) was correct in allocating *mullah* from Harar to a larger species, *A. dimidiatus*, widely sympatric with *A. cahirinus*, then the four larger animals from the Blue Nile may represent *A. dimidiatus*, but this must be considered very provisional until these two species can be more adequately delimited.

The single animal from Lake Chamo has a very greyish pelage and a small skull (upper molar row 4·3 mm, condylobasal length 25·0 mm) and is likely to represent *A. cahirinus*.

Genus ***ARVICANTHIS***—Grass rats

Arvicanthis niloticus abyssinicus (Rüppell)

Debra Markos: four trapped in low, grazed *Acacia* scrub. The single female was pregnant (four embryos).

Dessie: ten from 18 km N.W. of Dessie, trapped on a rocky bank beside a marsh at 2700 m (from Wellcome Parasitology Unit no. 2).

Addis Alem: one collected by Dr Aklelu Lemma.

The animals from Debra Markos could be referred to *fluvicinctus* Osgood, but this is unlikely to be separable from *abyssinicus*. It was based entirely on the longer upper molar row of animals from west of the Blue Nile and the present series from Debra Markos and Dessie, on either side of the Blue Nile, show considerable overlap in this character. The specimens from Debra Markos are, however, distinguished from the Dessie series by an overall suffusion of yellowish brown whereas the Dessie animals are almost pure grey.

These are all dark-bellied animals and most have a distinct narrow mid-dorsal stripe. Other Ethiopian forms that are probably conspecific are *blicki* Frick (S. Chilalo Mts), and *saturatus* Dollman (Guma, Didessa River).

Arvicanthis lacernatus (Rüppell)

Harar: one from the Bisidima River, trapped in grazed thorn scrub.

Dessie: seven from 31 km N.W. of Dessie, trapped in a dry river valley at 2000 m (from Wellcome Parasitology Unit no. 2).

Lake Abbaya: seven from Arba Minch, S.W. of lake.

Awash: parts of ten skulls of a large *Arvicanthis*, probably this species, from one of the lava caves. One skin and skull, of an animal trapped in the National Park, received on loan from the park museum.

There seems to be good reason to recognize two species of large *Arvicanthis* in Ethiopia and in adjacent regions of Sudan, Uganda and Kenya, although much remains to be done to assess their variability. The present species has the underparts grey, rather sharply demarcated from the brown of the flanks. The grey of the belly may be quite dark, as in the series from the Dessie region, or may be suffused with brown in the midline as in the animal from Harar, but it is never speckled like the dorsal pelage as it is in most *A. niloticus*. *A. lacernatus* lacks a clearly defined dorsal stripe, and there is a tendency for the rump and hind legs to be unspeckled and tinged with orange brown. These characteristics are seen in fairly extreme form in the specimen from Harar; in the series from Lake Abbaya the brown on the rump is less distinct whilst in the series from Dessie it is absent altogether and the ventral pelage is a uniform dark grey. The brown colour on the rump in this species is very evenly distributed and seems quite distinct from the sporadic erythrism that seems to be a characteristic of *A. niloticus*. The specimen of *A. niloticus* from Addis Alem, for example, has on the belly a large irregular patch of hair with the basal parts chocolate brown instead of the usual slaty grey, and the tips yellowish brown instead of pale cream.

The specimen from Harar agrees very closely with the type of *pelliceus* Thomas (from Lake Tana) which Osgood (1936) maintained was a synonym of *lacernatus*. Other Ethiopian forms that are probably conspecific are *zaphiri* Dollman (Guma, Didessa River), *mearnsi* Frick (Awash) and perhaps *raffertyi* Frick (Gardula). It is possible that another synonym this species is *Isomys testicularis* Sundevall, 1843 from Bahr-el-Abiad, Sudan.

There is no evidence amongst the present collection of the two species being strictly sympatric in Ethiopia, but de Beaux (1930) recorded both from a single locality in Eritrea, and Heller (1911) described both species from Rhino Camp, N.W. Uganda (as *A. jebelae* and *A. rubescens*).

Arvicanthis somalicus Thomas

Awash: parts of 69 skulls from the lava caves; one animal shot by day in dry *Acacia* scrub, but only the skull preserved; six animals subsequently trapped by

D.W.Y. in December 1970 at Metahara, in heavily grazed grassland with patches of *Acacia* scrub.

This species, described from northern Somalia, does not appear to have been recorded hitherto in Ethiopia. Allen (1939) listed it as a distinct species, with *chanleri* and *reptans* from northern Kenya as races, but Misonne (1968) recognized only one species of *Arvicanthis*, presumably considering *somalicus* to be no more than subspecifically distinct from *A. niloticus*.

The skulls from the Awash caves were the first indication of two sympatric species differing in size (fig. 3), and agreeing respectively with specimens of *A. somalicus*

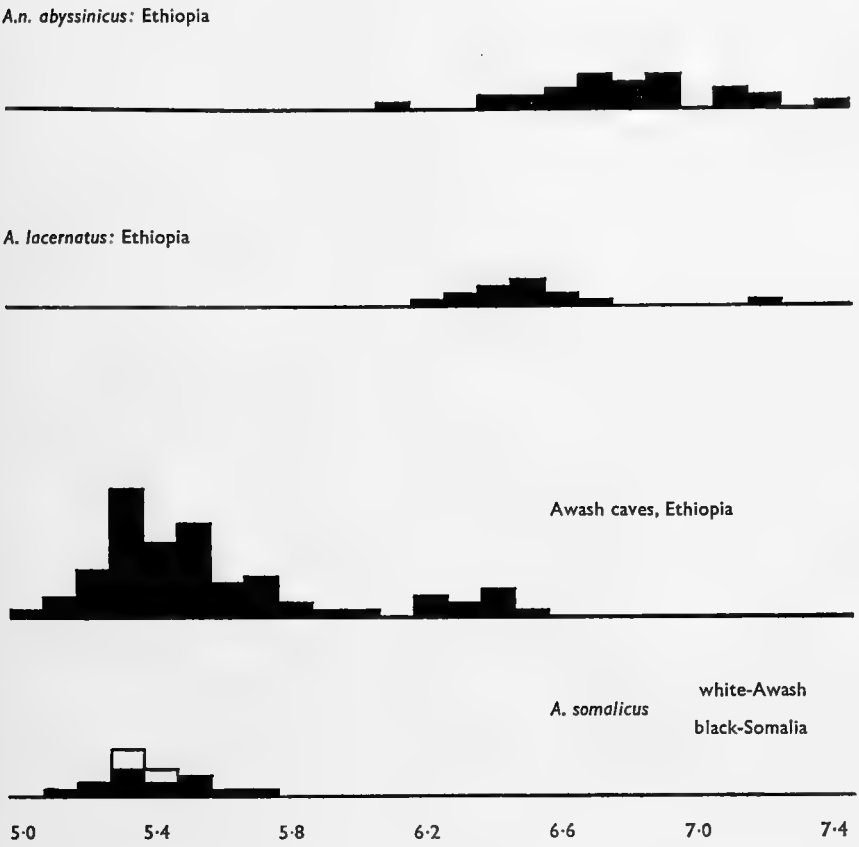


FIG. 3. Length of upper molar row (at maximum of crown) of *Arvicanthis* spp.

from Somalia and of *A. lacernatus* from elsewhere in Ethiopia. This was confirmed by the trapping of six specimens of *A. somalicus* nearby at Metahara in 1970.

These specimens agree very closely with *A. somalicus* from Somalia, including the type, except that the pelage is less yellow. The difference in size, especially of the tooth-row, is sufficiently clear to leave no doubt that there is sympatry of two species at Awash. (Besides the large skulls in the cave sample, we have subsequently seen a specimen of *A. lacernatus* trapped at Awash, which had a tooth-row of 6·3 mm.)

A. somalicus can therefore be considered specifically distinct from *A. niloticus* and *A. lacernatus*, and this record extends its known range by about 400 km westwards from the nearest localities in northwestern Somalia represented by specimens in the British Museum (around Hargeisa). The types of *chanleri* Dollman and *reptans* Dollman, both from the Northern Uasso Nyiro district of Kenya, also fall well within the range of these Ethiopian specimens, with molar rows of 5·6 and 5·5 mm respectively, but considerably more work needs to be done to establish to what extent these small forms are sympatric with larger ones in Kenya.

Externally *A. somalicus* and *A. lacernatus* are very similar at Awash. The best distinguishing characters are probably the greater amount of yellow in the dorsal pelage of *A. lacernatus*, especially marked on the rump, and the longer hind feet (22–23 mm in *A. somalicus*; about 30 mm in *A. lacernatus*).

The five available skins of *A. somalicus* from Awash are all of rather young animals, with the teeth scarcely worn, and therefore the other external measurements (head and body 93–106 mm; tail 88–105 mm) are probably below adult size. The ventral pelage of *A. somalicus* resembles that of *A. lacernatus* in being pale grey, rather sharply demarcated from the brown of the flanks.

Dasymys incomtus (Sundevall)—Shaggy rat

Bahar Dar: one trapped in wet grassland with scattered thickets.

Bahar Dar is close to the type locality of *D. i. griseifrons* Osgood, but this specimen does not show the grey forehead and face described for *griseifrons*. The only other examples of this species from Ethiopia in the British Museum are single specimens from Nono, upper Omo and Wodessa River, Guma. Delany & Neal (1963) also reported this species from damp habitats in Uganda ('swamps, reed beds and river valleys') and mentioned that it occurs above 4000 m on Ruwenzori.

Lemniscomys striatus (L.)—Striped mouse

Blue Nile Gorge: one 10 km east of Caroarsa River; four at mouth of Didessa River. These were all trapped in long grass on the bank of the river.

The only previous records of this species in Ethiopia appear to be from Nono, 150 km south of the Blue Nile (the type of *wroughtoni* Thomas), from the Urgessa River (an upper tributary of the Didessa River) and from Delbena River, Konso (?near Mega in the extreme south). The two skins from the Blue Nile have the normal yellowish brown ground colour with only the mid-dorsal stripe dark, closely resembling *L.s. massaicus* (Pagenstecher) of Kenya and the skin from Konso, and quite different from the adjacent *L.s. wroughtoni* which has all the dark stripes virtually black. The type and only available specimen of *wroughtoni* came from 3600 m; the single specimen from the Urgessa River, at 2300 m, is considerably less dark, in fact intermediate between *wroughtoni* and the normal specimens from the Blue Nile at the mouth of Didessa River at about 800 m.

The Blue Nile animals resemble the East African *L.s. massaicus* and differ from West African forms, e.g. *L.s. striatus*, in having the lateral white stripes very bold and continuous. They differ from most *L.s. massaicus* in having the second white stripes (away from the mid-dorsal line) very well marked whereas these stripes are very fragmentary in *massaicus*.

Lophuromys flavopunctatus Thomas—Harsh-furred rat

Bahar Dar: seven trapped in thickets in wet grassland.

Debra Markos: one trapped in low, grazed *Acacia* scrub.

Ghimbi: two adults and three nestlings.

Harar: two trapped amongst thorn scrub at Bisidima River.

Dessie: two from 18 km N.W. of Dessie at 2700 m, trapped on the edge of a marsh (from the Wellcome Parasitology Unit no. 2).

Addis Ababa: one from the British Embassy compound (from Wellcome Parasitology Unit no. 2); one from Meta Abo, Sabata, c. 20 km S.W. of Addis Ababa.

The specimens from Harar appear to differ from the series from the highlands only in the lighter and brighter orange-brown colour of the proximal zone of the dorsal hairs. These can probably all be attributed to *L.f. flavopunctatus*. The single skin from Addis Ababa differs from all the others in being more coarsely speckled above due to longer subterminal light bands on the hairs.

The locality at Harar, although close to the River Bisidima, is an unusually dry habitat for this species which is more characteristic of montane forest or moist scrub.

One female from Harar and that from Debra Markos were pregnant, each with five embryos.

Genus ***MUS***—Pygmy mice

Mus mahomet Rhoads

Debra Markos: two trapped in small thicket surrounded by grazed grassland.

Dessie: one from 18 km N.W. of Dessie at 2700 m on a steep rocky hillside grazed by goats; two from 31 km N.W. of Dessie at 2000 m (all from the Wellcome Parasitology Unit).

This is a rather distinctive species, apparently confined to Ethiopia and the adjacent part of Somalia. It is a fairly large grey-bellied form with yellow lines bordering the grey and a faint mid-ventral yellowish stripe.

Mus tenellus (Thomas)

Blue Nile Gorge: four from 10 km west of Mabil, trapped in dry scrub; one 10 km east of Caroarsa River, trapped amongst tall, wet grass.

Awash: two, probably of this species, in dry *Acacia* scrub close to riverine woodland.

The group of small, white-bellied *Mus* (or *Leggada*) badly needs revision. These have been compared with the type of *tenellus* (from Roseires on the Sudanese Blue Nile) and there seems little doubt that at least the Blue Nile animals can be allocated to that form.

Mus ?pasha (Thomas)

Blue Nile Gorge: eight from 10 km west of Mabil, trapped in grassland adjacent to permanent riverine vegetation.

These are white-bellied mice considerably larger than *M. tenellus*, with head and body length of 69–85 mm (49–65 mm in *M. tenellus*), hind feet of 14–15 mm (12–13 mm in *M. tenellus*), and upper molar row of 3·7 mm (two specimens; 3·1 and 3·0 mm in two *M. tenellus*). *Leggada pasha* was described from the Uele District, N.E. Congo but was treated by Osgood (1936) as a race of *Mus proconodon* Rhoads from Somalia. Setzer (1956) did not record either of these forms from the Sudan.

Genus ***PRAOMYS***—Soft-furred rats

Praomys albipes (Rüppell)

Debra Markos: one caught by hand in camp amongst low *Acacia* scrub.

Bahar Dar: two trapped in thickets in wet grassland.

Blue Nile Gorge: one caught on a boat, 30 km below Portuguese Bridge near Mota at 11° 12′N, 38° 05′E, altitude 1400 m.

Addis Ababa: nine from about 48 km west of Addis Ababa (from Wellcome Parasitology Unit).

Dessie: one from 31 km N.W. of Dessie (from Wellcome Parasitology Unit).

Lake Abbaya: eight from the Bonchi Valley, west of the lake at 2900 m.

This is a clearly defined species, formerly placed in the genus *Myomys*, confined to the Ethiopian Highlands except for an isolated and only doubtfully conspecific form, *P.a. fuscirostris*, in Sudan. These specimens, like all those recorded from Ethiopia, belong to *P.a. albipes*. All are from the plateau, between 1400 and 3000 m.

Praomys fumatus brockmani (Thomas)

Harar: one trapped in thorn scrub beside a dry river bed 60 km east of Harar on Jiggigga road.

This specimen agrees well with the type of *brockmani* from northern Somalia and is distinctly paler than *P.f. allisoni* Hayman from central Ethiopia. This species was recorded from the Harar area by Ingersol (1968).

Praomys (Mastomys) natalensis (Smith)

Blue Nile Gorge: one skull found at mouth of Guder River; one trapped in dry scrub 10 km west of Mabil; four trapped in long grass at the edge of riverine forest at the mouth of the Azir River; eleven from the mouth of the Didessa River, in long grass on the river bank and in maize cultivation near the village.

Bahar Dar: one trapped in thicket in wet grassland.

Ghimbi: one 24 km north of Ghimbi, in long grass.

Harar: two from Bisidima River, in dry, grazed thorn-scrub.

Awash: four from dry *Acacia* scrub; a few skulls from the lava caves.

Lake Abbaya: eight from the following localities. Bonchi Valley, west of lake, 2900 m; Collufo River, between Lake Abbaya and Lake Chamo; mouth of Darsi River.

Little Abbai: six collected.

Osgood (1936) recognized two species of '*Mastomys*' in Ethiopia, which he called *M. coucha lateralis* (Heuglin) and *M. macrolepis* (Sundevall). The latter he described as having a longer tail, shorter hind feet and paler ventral pelage, and recorded from the Blue Nile Gorge and Lake Tana (the type locality is Roseires on the Blue Nile in Sudan). Setzer (1956) listed *macrolepis* as a race of *M. natalensis* (*M. coucha*), although he recognized two sympatric species of *Mastomys* elsewhere in Sudan. In the present collection the animals from the Nile Gorge have the tail longer than the head and body (measured from the anus) with four exceptions out of 16 (mean 102·4% of head and body); those from Awash and Harar have the tail shorter than the head and body in five out of six animals (mean 94·7%). The Nile animals have the ventral pelage paler than the eastern ones, but there is no difference in length of hind foot: mean of 24·6 mm in the gorge, 24·5 mm in the eastern samples. The single skin from Bahar Dar on Lake Tana is dark-bellied with a short tail as in the eastern samples.

These are all tentatively referred to *P. natalensis*, but this group badly needs revision, especially in view of the demonstration of sibling species with very different chromosome complements elsewhere in Africa (Matthey, 1966).

Rattus rattus alexandrinus (Geoffroy)—House rat

Ghimbi: three collected in or around the town.

Harar: three from the Bisidima River.

Lake Abbaya: six from near Soddu.

These are called *R.r. alexandrinus* following the revision by Schwarz and Schwarz (1967) who treated *Mus samharensis* Heuglin (Ethiopia) and *Mus kijabius* Allen (Kenya) as synonyms.

Dendromus mystacalis Heuglin

Blue Nile Gorge: one from mouth of Guder River, caught by hand in the camp near steep rocky hillside with thick bush; one at mouth of Didessa River, caught by hand under bushes on a small island. Both were in the riverine forest strip.

This is a poorly known species in Ethiopia although it appears to have a wide distribution through much of Africa. These specimens have a very slight darkening in the mid-dorsal area but no black stripe, and a similar specimen is in the British Museum from 230 km south of Addis Ababa. Specimens from Dangila and Lake Tana on the other hand mostly have a clear dorsal stripe.

Otomys typus (Heuglin)

Debra Markos: one trapped by day in low, grazed *Acacia* scrub.

This specimen represents the nominate subspecies, described from the Simien Mountains.

Family **GLIRIDAE**—Dormice

Graphiurus murinus ?internus Dollman

Blue Nile Gorge: one at the mouth of the Fincha River, trapped in riverine forest, 45 cm off the ground in dry bushes.

There are very few previous records of *Graphiurus* from Ethiopia. These appear to be from Mt. Amar Cocche, Omo Valley, recorded as *Claviglis brockmani internus* by de Beaux (1943); Saganeita, Eritrea, recorded as probably *C. orobinus* by de Beaux; Guri Dagono and Sidamo, Arussi, recorded as *G.m. saturatus* by Hayman (1960); and Gara Mullata, Harar, recorded by Ingersol (1968) without allocation to subspecies. Only the skin from Guri Dagono has been available for comparison. The present specimen appears identical, but with respect to colour these specimens are much closer to the type of *G.m. internus* Dollman from northern Kenya than to the darker *G.m. saturatus* from Mount Elgon. The skull is, however, rather large (condylobasal length 23·3 mm as compared with 20·7 in the type of *internus*, a slightly older animal judging by the teeth).

This genus has never been adequately revised and the allocation of all named forms from northeastern Africa to *G. murinus* (type locality Cape of Good Hope) must be considered very tentative. A form described from Senaar on the Blue Nile in Sudan, *Myoxus orobinus* Wagner, 1845, may be relevant, but no further specimens have been reported from that region of Sudan and the original description is inadequate.

Family **RHIZOMYIDAE**—Mole-rats

Tachyoryctes splendens (Rüppell)

Dessie: one from 18 km N.W. of Dessie (from the Wellcome Parasitology Unit no. 2).
Addis Ababa: one from Meta Abo, Sabata, c. 20 km S.W. of Addis Ababa.

Lake Abbaya: two from the Bonchi Valley at 2900 m; one from Mount Gugi (2400 m); and three from Arba Minch.

These can probably all be referred to *T.s. splendens*, being rather smaller than *T.s. cheesmani* Thomas from Lake Tana.

Tachyoryctes macrocephalus hecki Neumann and Rümmler

Bale Mountains: one (skin and skull) from Dinshu (=Gurie), Ueb Valley, at 3500 m (from Mr J. H. Blower); a fragmentary skull from an eagle's nest 30 km south of Dinshu at 3800 m (sent by Mr L. H. Brown); a complete skull from Batu (6° 55'N, 39° 47'E, 4150 m) collected by Mr H. F. Mooney. Mr Blower (in litt.) also saw colonies of this species at 3800 and 4000 m in the same area, apparently confined to 'open moorland where the grass is very short, often in relatively damp places, sometimes near streams'.

This is a very large mole-rat, about twice the size of the common *T. splendens*. Both the nominate race (from Shoa) and *T.m. hecki* appear to be known only from the original specimens, namely three syntypes of *macrocephalus* (in Berlin, Frankfurt, and London) and the type of *hecki* in Berlin.

The type locality of *hecki* was given as 'Abakkara, etwa 150 km westlich des Abassi Sees in Grenzgebiet zwischen Djamdjam und Arussi Galla gelegen'. Assuming that 'Abassi See' is Lake Awusa, the 'westlich' would seem to be an error for 'ostlich'. This would place it not only between Djamdjam and Arussi but close to the locality of the records reported here.

The present specimens agree with the description of *hecki*, and differ from the London syntype of *macrocephalus*, in having the rostrum and upper incisors relatively small (Table 1). This difference is very marked and suggests that these might prove to be genuinely discrete subspecies or even species, perhaps isolated by altitude. Even in *T.m. macrocephalus* the incisors are relatively smaller than in the small *T. splendens*, suggesting a less fossorial habit, and this is supported by the sight records, the animals being described as marmot-like and frequently visible on the surface (J. H. Blower, in *litt.*).

There is an old record of '*Tachyoryctes macrocephalus*' from Kita in the upper part of the Senegal basin (now in Mali) (Rochebrune, 1883). It was described as 'plus commune . . . dans les environs de Kita, où elle habite les crevasses des rochers et les pentes sablonneuses des collines boisées; les Européens la désignent sous le nom de Marmotte'. It seems probable that this account really refers to the gundi, *Felovia vae* (Lataste), which was not otherwise mentioned by Rochebrune and was first discovered by Lataste in the Felou Hills, about 250 km northwest of Kita, and described by him in 1886.

Ignoring this probably erroneous record, *T. macrocephalus* is endemic to the Ethiopian plateau.

TABLE 1

Measurements of *Tachyoryctes macrocephalus*

	T. m. hecki				*T. m. macrocephalus*		
	BM 68.856	BM 70.746	Type of *hecki**	BM 71.876	BM 42.8.15.1	Senck. Mus. 728*	Berlin*
Length of head and body (from dry skin)	c. 400						
Length of hind feet	33				34		
Condylobasal length				64·0			
Width across premaxillae	11·2	12·2	c. 10·9	11·8	14·1		
Combined width of upper incisors (near tip)	7·1	7·0	7·2	7·0	9·5	8·6	9·5
Interorbital width	5·7	6·0	6·2	6·2		5·7	6·3
Length of nasals	29·6	30·2		28·3	27·9		
Upper molar row (alveolar)	12·0	11·8	13·0	12·1		12·0	12·2
Lower molar row (alveolar)	13·5		13·8	13·8	13·1	13·3	13·7
Length of mandible	43		c. 42	43	c. 45	43	

* From Neumann & Rümmler, 1928.

Family **THRYONOMYIDAE**—Cane rats

Thryonomys gregorianus (Thomas)

Blue Nile Gorge: one damaged skull from a cave 10 km W of Mabil; possible sightings at the Didessa River.

Wollega Province: one specimen from Bako in Addis Ababa Museum (skull and colour photo of mounted skin examined by G.B.C.).

Ilubabor Province: one skin from Gambela collected by Dr J. Ash in March 1969.

The Blue Nile specimen was on the surface of the floor of a cave covered with bat and hyrax guano and therefore must be very recent. These appear to be the first records of *Thryonomys* from Ethiopia, and in Sudan the only record of *T. gregorianus* is from the Didinga Mountains on the southern border. These skulls agree closely with the type of *gregorianus* (from central Kenya) and differ from the type of *harrisoni* Thomas & Wroughton from southern Sudan in having the nasals short and wide; the posterior processes of the premaxillae wide and rounded (in dorsal view); and the zygomatic parts of the lachrymals elongate. The skin from Gambela could conceivably be *T. harrisoni* if that is distinct. Both skins have the short tail (not extending beyond the hind feet when these are extended backwards) characteristic of *T. gregorianus* and *T. harrisoni* in contrast to the very much longer tail of *T. swinderianus*. The skin from Gambela is of a young animal with the following measurements: head and body 329; tail 73; hind feet 71; and ear 25 mm.

Setzer (1956) treated *T. gregorianus* and *T. harrisoni* as specifically distinct, recording both from southern Sudan. Misonne (1968) recognized only two species in

the genus, *T. swinderianus* and *T. gregorianus*, presumably treating *harrisoni* as conspecific with *gregorianus*, but in view of the cranial differences and the small numbers of specimens available it seems wise to treat them as provisionally distinct.

A subfossil *Thryonomys* from a mesolithic site at Khartoum, Sudan has been described as *T. arkelli* by Bate (1947, 1949). Bate considered it more closely related to the larger *T. swinderianus* than to *T. gregorianus* or *T. harrisoni* and a re-examination of the type supports this view. It differs from the types of *T. gregorianus* and *T. harrisoni* and from the Ethiopian specimens in its slightly larger size, prominent masseteric knob and robust anteroventral root of the zygomatic arch.

Family **HYSTRICIDAE**—Porcupines

Hystrix cristata L.—Crested porcupine

Lake Chamo: one from northeast of lake, in the 'White Grass' area.

Blue Nile Gorge: quills found at the Mugher, Guder, Fincha and Caroarsa Rivers.

Awash: quills found in the lava caves.

H. cristata is here considered to include the East African *galeata* (Corbet & Jones, 1965).

Order **CARNIVORA**

Family **CANIDAE**

Lycaon pictus (Temminck)—Hunting dog

Lake Abbaya: one shot near Soddu in 1964.

Canis aureus L.—Golden jackal

Luma, Didessa Basin: a skull received from Mr John Blower is probably of this species. The animal was shot in a cultivated clearing in bamboo forest at 9° 40′N, 35° 55′E, 2000 m.

Dangila: one shot between Dangila and Engiabara.

Little Abbai: two collected.

Otocyon megalotis (Desmarest)—Bat-eared fox

Harar: one from the Bisidima River; one from 60 km east of Harar on the Jiggigga road; eight others seen in this area.

Awash: a skull was found on the floor in one of the lava caves.

Family **MUSTELIDAE**

Ictonyx striatus (Perry)—Zorilla

Awash: one seen at night.

Addis Ababa: one dead on the main road south-east from Addis Ababa to Shashamane.

Family **VIVERRIDAE**

Genus ***GENETTA***—Genets

Genetta genetta (L.)

Harar: one from the Bisidima River; one from 60 km east of Harar on the Jiggigga road.

Genetta ?tigrina (Schreber)

Ghimbi: one from 24 km east of Ghimbi.
Lake Chamo: one from northwest of lake.
Lake Abbaya: one from Arba Minch, southwest of lake.
The three skins collected are very similar in colour and pattern. According to Coetzee (1967) the Ethiopian race is *G.t. schraderi* Matschie. The taxonomy of this group of genets is in a very provisional state. It is possible that the northern forms of the *tigrina* group, including *schraderi*, represent a separate species, *G. rubiginosa*. A third species of genet recorded from Ethiopia, but not represented in the present collections, is *G. abyssinica* (Rüppell) which Coetzee (1967) separated subgenerically from *G. genetta* and *G. tigrina*.

Ichneumia albicauda (G. Cuvier)—White-tailed mongoose

Bahar Dar: one collected.
Ghimbi: three collected.
Lake Abbaya: two from Arba Minch.
Lake Chamo: three from northwest of lake; two from 12 km south of Gardulla, south of the lake.
Blue Nile Gorge: one seen at Mabil.

Herpestes sanguineus Rüppell—Slender mongoose

Lake Chamo: one from west side of lake; one from northeast of lake.

Viverra civetta Schreber—Civet

Ghimbi: one from 10 km east of town.
Lake Abbaya: one from near Soddu; one from Arba Minch.

Family **HYAENIDAE**

Proteles cristatus (Sparrman)—Aardwolf

Awash: the remains of five animals were recovered from one of the lava caves, one as a complete skeleton and four skulls.
The aardwolf has a very wide distribution in Africa, but it is a very elusive animal and is seldom recorded. Ingersol (1968) reported it from the Afden Plain just east of the Awash and at Amarresa in the Harar district.

Crocuta crocuta Erxleben—Spotted hyaena

Harar: about 15 hand-fed by the 'hyaena man' at dusk outside the city.
Ghimbi: one dead on the main road east of the town.
Debra Markos: up to six seen around the town.

Family **FELIDAE**

Felis silvestris libyca Forster—Wild cat

Harar: one from the Bisidima River.
Bahar Dar: one collected.
Blue Nile Gorge: one from Shafartak.

Felis serval Schreber—Serval

Degen, Gojjam: one collected.
Ghimbi: one collected.
Little Abbai: two collected.
These all have the ground colour of the pelage yellowish as in *F. s. hindei* Wroughton from Kenya which they closely resemble, and are not nearly so pale as in the type of *F.s. tanae* (Pocock, 1944) from Lake Tana.

Panthera pardus (L.)—Leopard

Blue Nile Gorge: one seen beside the river, between Shafartak and the Mugher; traces near the Caroarsa River.
Awash: two seen.

Panthera leo (L.)—Lion

Awash: two seen hunting together.
Blue Nile Gorge: unconfirmed report of a party near the mouth of the Guder River.

Order HYRACOIDEA

Procavia habessinica (Hemprich & Ehrenberg)—Large-toothed rock hyrax

Harar: two from Valley of the Rocks, 40 km east of Harar; two from 60 km east of Harar (all *P.h. erlangeri* Neumann).
Lake Langano: two from west side of lake (*P.h. alpini* (Gray)).
These two groups are so different in appearance that their conspecificity must be considered doubtful. The *P.h. erlangeri* agree closely with a series in the British Museum from Dire Dawa, about 50 km N.W. of Harar, and specimens were recorded from Harar by Neumann. These all have the head black with a rufous tinge, the dorsal pelage mottled yellow and black and the dorsal glandular spot scarcely visible. A very young animal (head and body 260 mm) has the head equally black but there is less yellow in the rest of the dorsal pelage.

The skins of *P.h. alpini* have the head much lighter, the dorsal pelage greyish brown and finely speckled, and the glandular streak prominently yellow. The yellow glandular streak distinguishes this form from *P.h. habessinica* from N.E. Ethiopia and from *P.h. scioana* (Giglioli), a very dark form from Ankober, Shoa, as well as from *P.h. erlangeri*.

In view of the many problems remaining to be solved in this genus it seems premature to assume these to be conspecific with the South African *P. capensis* as suggested by Ellerman & Morrison-Scott (1951).

Heterohyrax brucei brucei (Gray)—Small-toothed rock hyrax

Harar: two from 60 km east of Harar, at precisely the same locality as the *Procavia habessinica*.

Blue Nile Gorge: mandibles found at mouth of Guder River.

Lake Abbaya: two from Arba Minch; two from Arba Mondi, south of lake.

The specimens from Harar agree closely with the type of *brucei*. The form *hararensis* Brauer from near Harar was listed by Allen (1939) as a synonym of *somalica* Thomas from N. Somalia, described as smaller and paler than the type of *brucei*. It is unlikely that *somalica* will prove a valid subspecies, but in any case the specimens from Harar seem closer to *brucei* than to *somalica*. *H.b. hararensis* was diagnosed as smaller than *brucei* and distinguished from both *brucei* and *somalica* by greyish white ventral pelage. In fact the present specimens have quite dark yellowish buff undersides, one of them with an irregular pure white area of the chest and in front of the genitalia. The dorsal glandular streak is bright yellowish brown.

The specimens from Lake Abbaya in the Rift Valley are scarcely distinguishable from those from Harar.

Order TUBULIDENTATA

Orycteropus afer (Pallas)—Aardvark

Debra Markos: burrows seen.

Awash: one killed by a car on the track in the park.

Order PERISSODACTYLA

Family **EQUIDAE**

Equus burchelli boehmi Matschie—Common zebra

Lake Chamo: up to 96 counted in the 'White Grass' area.

Order ARTIODACTYLA

Family **HIPPOPOTAMIDAE**

Hippopotamus amphibius L.—Hippopotamus

Blue Nile Gorge: seen from the Fincha River westwards, including Wamet Ford (4), Azir to Caroarsa (12), Didessa (tracks, and several heard at hight). Heard also

in the vicinity of Tississiat Falls. A skull found at the mouth of the Azir River was preserved.

Awash: one seen on several occasions.

Lake Abbaya: two skulls were found and preserved.

Family **SUIDAE**

Phacochoerus aethiopicus (Pallas)—Wart hog

Lake Abbaya: six collected, two near Soddu and four from near Arba Minch.

Lake Chamo: group of nine seen in the 'White Grass' area.

Awash: two family parties of 4+ seen; a skull was found in one of the lava caves.

Potamochoerus porcus (L.)—Bush pig

Lake Abbaya: one from south of the lake.

Family **BOVIDAE**

Madoqua phillipsi hararensis Neamann—Phillip's dik-dik

Harar: three from 60 km east of Harar on the Jiggigga road.

Awash: numerous sight records, each of one or two animals only.

Madoqua guentheri Thomas—Günther's dik-dik

Lake Chamo: four from the 'White Grass' area.

Sylvicapra grimmia (L.)—Common duiker

Bahar Dar: one collected, and several others seen.

Little Abbai: two collected.

Lake Abbaya: one from near Soddu.

Sire, Wollega: skull preserved of a female killed on the main road from Ghimbi to Addis Ababa, between the towns of Sire and Bako at 9° 08'N, 37° 05'E.

Ourebia ourebi (Zimmerman)—Oribi

Blue Nile Gorge: four seen at night on the air-strip at Sirba.

Oreotragus oreotragus (Zimmerman)—Klipspringer

Blue Nile Gorge: two seen between the Guder and Fincha Rivers and two between the Fincha River and Wamet Ford.

Harar: two seen in the Valley of the Rocks.

Kobus defassa (Rüppell)—Waterbuck

Awash: several, including a party of four.

Lake Chamo: a herd of 16 in the 'White Grass' area.

Alcelaphus buselaphus swaynei (Sclater)—Common hartebeest

Lake Chamo: up to 104 counted in the 'White Grass' area.
This subspecies is considered to be extinct in Somalia, and perhaps only 200 exist in Ethiopia (Simon, 1968).

Tragelaphus scriptus (Pallas)—Bushbuck

Ghimbi: two from 16 and 20 km east of Ghimbi.
Lake Abbaya: two from Arba Minch.
Blue Nile Gorge: one seen at Mabil.
Bahar Dar: one seen.
Awash: one seen.

Tragelaphus imberbis Blyth—Lesser kudu

Awash: seen in small numbers.

Tragelaphus strepsiceros (Pallas)—Greater kudu

Lake Chamo: two from between Lake Chamo and Lake Abbaya.
Lake Abbaya: one from Borodda, N.W. of lake.
Awash: up to 14 seen.

Litocranius walleri (Brooke)—Gerenuk

Awash: three seen.

Gazella soemmerringi (Cretzschmar) -Soemmerring's gazelle

Awash: large numbers seen, in groups of 50–100. One was collected and a skull was retrieved from one of the lava caves.
The specimen collected resembles the Somalian race, *G.s. berberana* Matschie, 1893, in its horn shape and extensive dark nose spot, and the Awash animals can probably be attributed to that race. This specimen does not agree well with Matschie's (1912) description of *G.s. erlangeri* from Awash.

Gazella granti Brooke—Grant's gazelle

Lake Chamo: two collected in the 'White Grass' area and 46 counted on one occasion.

Oryx gazella beisa (Rüppell)—Oryx

Awash: large numbers seen, including one herd of 150. Parts of two skulls were retrieved from the lava caves.

DISCUSSION

Zoogeographically, the fauna of Ethiopia (usually termed, to avoid confusion, the Abyssinian fauna) is noted for its peculiar caste. While much of the fauna is of a general East African type, including species with a wide distribution even down to the Cape Province, there is also a small proportion of species of Palaearctic affinities and a significant roster of endemic species as well. Moreau (1966) for the birds and Carcasson (1964) for the butterflies have commented on these peculiarities of the Abyssinian fauna when seen from the viewpoint of continental zoogeography, while Carpenter (1935), approaching the subject from a study of the Abyssinian butterfly fauna particularly, and including also relevant information from other groups, has discussed the different taxa.

The conspicuous endemicity undoubtedly results from the large area of high plateau included in Ethiopia and its isolation from neighbouring mountain areas—both Moreau and Carcasson note that two habitat types, montane woodland and montane grassland, contain most of the endemics in the groups they studied. The interplay of a variable Pleistocene climate and this montane area is presumably responsible for the Palaearctic element reaching Ethiopia—during glacial (pluvial) periods, montane habitats would have occurred at lower altitudes, and would have spread up the mountains along the Red Sea coast of the Sudan and Nubia. This spread of montane habitat in the glacial periods would also account for another peculiar zoogeographical relationship of some Abyssinian fauna, that element which is of general montane type and may as a result have affinities with the fauna of the Cameroon Highlands of West Africa.

Any zoogeographical analysis of the mammalian fauna has hitherto been mainly confined to the larger mammals—see for example Blower (1968), Scott (1958) and Glass (1965)—and can be usefully illustrated by the maps showing the range of individual species throughout Africa in Dorst & Dandelot (1970). In the following analysis the smaller mammals are also considered, although many taxonomic problems remain to be solved before this can be quantified precisely at the levels of the species and subspecies.

The East African savanna and steppe element

This is the dominant element in southern and western Ethiopia, in the Rift Valley and in the valley of the Blue Nile. Many of the species concerned have wide distributions throughout the savanna zone from West Africa to Tanzania and further south, e.g. the giraffe *Giraffa camelopardalis*, the hartebeest *Alcelaphus buselaphus* and the striped mouse *Lemniscomys striatus*. Species of this group vary in the extent to which they penetrate Ethiopia. *L. striatus* occurs in the valley of the Blue Nile and its tributaries but does not appear to occur in the Rift Valley. *A. buselaphus* on the other hand extends through the Rift Valley to the Awash Valley. Grant's gazelle *Gazella granti* shows another pattern in that it reaches from Kenya into the southern part of the Rift Valley but is replaced by a related species, *G. soemmerringi*, in the northern part of the rift.

Small mammals falling into this general group, all reaching their north-eastern

limit in Ethiopia, are *Graphiurus murinus*, *Praomys fumatus*, *Elephantulus rufescens* and *Galago senegalensis*. Species with a similar range, but also reaching north of Ethiopia, are *Acomys* spp., *Arvicanthis niloticus*, *Hystrix cristatus*, *Lepus capensis*, *Crocidura flavescens* s.l. and *Felis silvestris*.

The Somalian arid zone element

Somalia is an area with a considerable degree of endemicity amongst the dry steppe fauna, and some of these species reach into eastern Ethiopia. The most sharply differentiated (endemic genera) are the gundi, *Pectinator spekei*, the naked mole-rat, *Heterocephalus glaber*, which reaches west as far as Shoa, the dibatag, *Ammodorcas clarkei*, which just reaches eastern Ethiopia, the beira, *Dorcatragus megalotis*, and the gerbil *Microdillus peeli*, the last two unrecorded from Ethiopia. Another group comprises species that are more closely related to widely distributed savanna or steppe species, e.g. *Gazella soemmerringi* which has a wide range, reaching round the northern edge of the Ethiopian highlands to the Sudan, the dik-dik *Madoqua phillipsi* and the grass-mouse *Arvicanthis somalicus* here recorded from Awash. Comparable Somalian species that do not appear to have been recorded in Ethiopia are the elephant shrew *Elephantulus revoili* and the hedgehog *Erinaceus sclateri*.

The Palaearctic element

This is a very small element in the mammalian fauna comprising the ibex, with *Capra ibex nubiana* in the Red Sea Hills and a southern isolate, *C.i. walie*, in the Simien Mountains; the wild ass *Equus africanus* in the Danikil Desert; and the shrew *Suncus etruscus*, here reported from the plateau but in its Mediterranean range a species of the drier lowlands. It is probable that the hedgehog *Paraechinus aethiopicus*, a species with a Saharan and Arabian distribution, is also present in northern Ethiopia. All these are tolerant of dry conditions. The ass probably had a continuous range from North Africa to Somalia in recent times, but the ranges of the ibex and the shrew are of a relict character, the latter showing a considerable degree of disjunction although it is an easily overlooked species and may still be found in intervening regions.

Among the birds of Ethiopia, the most notable Palaearctic immigré is the chough *Pyrrhocorax pyrrhocorax*, while the endemic owl *Asio abyssinicus* is considered a close relative of the northern *A. otus*; other Palaearctic birds listed by Moreau (1966) include the grebes *Podiceps caspicus* and *P. ruficollis*, the lammergeier, *Gypaetus barbatus*, Alpine swift, *Apus melba*, and quail *Coturnix coturnix*, which occur also into Kenya. Among the butterflies Carcasson (1964) and Carpenter (1935) list seven or eight species of Palaearctic affinity, including the endemic 'speckled wood', *Pararge madarakal*, and *Pieris brassicoides*, found also in Tanganyika.

The East African montane element

In spite of the very great distances separating the montane forest and grassland habitats of Ethiopia from comparable habitats further south, e.g. in the Kenya

highlands and Mount Elgon, there are several forms showing very little differentiation between these segments of their ranges. Examples amongst the rodents are *Lophuromys flavopunctatus*, *Lophiomys imhausi*, *Otomys jacksoni* and *Tachyoryctes splendens*. Some of these species, however, have moderately wide ecological requirements, e.g. *L. flavopunctatus* which is here recorded from seasonally dry habitats near Harar although it is more strictly confined to forest farther south. A lesser known rodent with a highly disjoint distribution is *Colomys goslingi*, known from swampy habitats in Cameroon, N.E. Congo, Kenya and the Ethiopian plateau where it is known from a single specimen previously believed to represent an endemic genus *Nilopegamys* (see Hayman, 1966). The mountain reedbuck, *Redunca fulvorufula*, also has a highly disjunct range with isolates in S. Africa and perhaps in Cameroon, but it is tolerant of fairly dry habitats.

Amongst the birds and butterflies there are likewise a number of species with strikingly disjunct distributions in various montane areas in East Africa, and across in some cases to the Cameroon Mountains and in others as far as Cape Province. The weaver *Cryptospiza salvadori*, for example, occurs in isolated patches of Ethiopia, Uganda, Kenya and Tanzania, while the babbler *Alcippe abyssinicus* occurs in these areas and in the Cameroons as well (Moreau, 1966). Carpenter (1935) listed about ten butterflies with similar distributions.

The endemic element

Endemic Ethiopian species are confined to the highlands and especially to the high montane grasslands which have presumably had the longest period of isolation and until recent deforestation were presumably much more sharply isolated from any comparable lowland habitats than they are today. The species concerned are the gelada baboon, *Theropithecus gelada*, the Simien fox, *Canis simensis*, the mountain nyala, *Tragelaphus buxtoni*, the genet *Genetta abyssinica*, the giant mole-rat *Tachyoryctes macrocephalus*, and the murid rodents *Stenocephalemys albocaudata*, *Muriculus imberbis*, *Dendromus lovati*, *Praomys albipes*, and *Pelomys dembeensis*. All these are well defined species, and three are currently considered endemic genera, namely *Theropithecus*, *Stenocephalemys* and *Muriculus*. It is possible that further endemic species occur in the genera *Crocidura*, *Procavia*, *Lophuromys*, *Arvicanthis*, *Praomys*, *Mus* and *Pelomys*, but further revision is needed to clarify their relationships with neighbouring forms.

All of these endemics belong to African rather than to Palaearctic groups, and all have their closest relatives in Ethiopia or in adjacent parts of East Africa. There are probably about 135 species of mammals in Ethiopia (excluding bats and marine species) and the eleven clear-cut endemics listed above therefore represent about 8·5% of the fauna, a figure that is likely to increase somewhat with further revision. Of the estimated 124 non-endemic species, about 16 are montane species whose Ethiopian populations are widely isolated from the rest of the range whilst the remainder, the great majority, are the more xerophilous species with ranges extending relatively unbroken into surrounding territories.

Carcasson (1964) listed at least 8 endemic butterflies (*Pararge maderakal*, *Papilio*

aethiops, Mylothris mortone, Bicyclus aethiops, Charaxes phoebus, Acraea oscari, A. ungemachi, A. safie) while Carpenter (1935) listed in all about 526 species from above 1500 m in Ethiopia; neither of these figures are complete, but they suggest an endemicity in the fauna of perhaps 2%. Among the endemic birds, Moreau (1966) mentioned the owl *Asio abyssinicus*, blue-winged goose *Cyanochen cyanopterus*, a swallow *Hirundo megaensis*, and the crow *Zavattariornis stresemanni*. In all, he suggested that there are 3 montane-forest and 21 montane non-forest endemic birds, while Urban & Brown (1971) listed 23 endemics in a total avian (breeding) fauna of 655 species. This would suggest an endemicity of about 3·5%.

Summary of Zoogeographical Affinities

It is clear from what little information has been presented above that the mammal fauna of Ethiopia shares with the better known bird and butterfly faunas the zoogeographical peculiarities of a conspicuous endemic element, a Palaearctic element, and also an element of discontinuously distributed montane animals. There is a suggestion that among the mammals the endemic element is greater and the other two elements fewer, and it is tempting to speculate on the role of relative mobility of the mammals as against the birds and butterflies. Unfortunately the mammalian faunas of both Ethiopia and other areas of importance are not sufficiently well known to be categorical about this—it may be relevant to note here that this paper records four species new to Ethiopia (*Crocidura niobe, Suncus etruscus, Thryonomys gregorianus* and *Arvicanthis somalicus*) and records several others that have been previously noted fewer than six times (*Tachyoryctes macrocephalus, Taterillus emini, Lemniscomys striatus, Praomys fumatus, Protcles cristatus*).

Fauna of the Blue Nile Gorge

Since the main object of the 1968 expedition was to carry out a scientific survey in the gorge of the Blue Nile, some concluding comments on the small mammals obtained there are justified. One point that was very evident in the field was the scarcity of small mammals—over nine hundred trap-nights were required to obtain 52 small mammals, or 17 trap-nights per specimen (for comparison, at Awash, about 5 trap-nights per animal, and at Bahar Dar 15 per animal, were required). From the species caught, it is evident that the small mammal fauna of the gorge is comparable with that found at Awash and east of Harar; among the species or genera common to both are *Crocidura ?sericea, Acomys dimidiatus, Heterohyrax brucei, Procavia habessinica* (on sight records only from the Blue Nile Gorge), *Tatera* sp. (*T. valida* in the Gorge, *T. robusta* in the East), *Mus tenellus*, and *Oreotragus oreotragus*.

By contrast, the collecting localities on the plateau (Ghimbi, Bahar Dar, Debra Markos) have in common *Lophuromys flavopunctatus*, and *Praomys albipes* was found at the two more northern of these. The presence in the Blue Nile Gorge of *Tatera valida, Lemniscomys striatus, Mus ?pasha* and *Acomys* spp. implies perhaps the incursion of an East African savanna element. While for human travel the Blue Nile Gorge represents a considerable barrier, so far as small mammals are concerned

it would seem rather to be a highway allowing dry-country, lowland species to penetrate deeply into the centre of Ethiopia.

ACKNOWLEDGEMENTS

Thanks are due to all those members of the Great Abbai Expedition and the previous expeditions who made these collections, and this report, possible. If this acknowledgement seems rather curt, full justice is done in the expedition reports. So far as the actual collection of mammals is concerned, particular thanks are due to Dr P. A. Morris, Dr M. J. Largen, and H. King. D.W.Y. would like to acknowledge the receipt of a staff travel grant from the University of Manchester. We are grateful also to Mr John Blower, Mr Leslie Brown, Dr R. Ashford and Dr Aklelu Lemma for sending specimens.

GAZETTEER

			Altitude (metres)	Dates of collecting
Abiu, Ilubabor	8°11′N	35°22′E	1500	January 1971
Addis Ababa, Shoa	9°00′N	38°45′E	2300	
Addis Alem, Shoa	9°03′N	38°25′E	2400	
Arba Minch, Gemu Gofa	6°04′N	37°40′E	1300	6 August–3 September 1966
Awash, Shoa	8°50′N	40°01′E	950	23–28 September 1968
Awash (lava caves), Shoa	8°56′N	39°57′E	950	28 September 1968
Azir River (mouth of)	10°29′N	36°25′E	800	20–22 August 1968
Bahar Dar, Gojjam	11°35′N	37°25′E	1830	11–14 September 1968
Bako, Wollega	9°08′N	37°05′E	1800	
Bisidima River, Harar	9°15′N	42°12′E	1500	20–21 September 1968
Bonchie Valley, Gemu Gofa	6°05′N	37°20′E	2700	1966
Caroasa River (near mouth)	10°07′N	36°12′E	600	23–24 August 1968
Collufu River (mouth), Gemu Gofa	6°04′N	37°40′E	1300	6 August–3 September 1966
Danghila, Gojjam	11°15′N	36°55′E	2000	
Darsi River, Gemu Gofa	6°15′N	37°50′E	1300	
Debra Libanos, Shoa	9°45′N	38°50′E	2300	
Debra Markos, Gojjam	10°20′N	37°50′E	2500	4–27 August 1968
Degen, Gojjam	10°10′N	38°05′E	2500	
Dessie, Welo	10°08′N	39°43′E	2700	
Didessa River (mouth of)	10°05′N	35°38′E	450	26–29 August 1968
Dim River (mouth of)	10°30′N	36°26′E	800	22 August 1968
Engiabara, Gojjam	10°58′N	36°58′E	2500	
Fantalle (Mt), Shoa	8°58′N	39°54′E	2000	
Filhoa, Awash, Shoa	9°00′N	39°58′E	1000	23–28 September 1968
Fincha River (mouth of)	10°03′N	37°20′E	1000	11–13 September 1968
Gambela, Ilubabor	8°15′N	34°35′E	600	
Ghimbi, Wollega	9°10′N	35°50′E	2150	22–31 August 1968
Guder River (mouth of)	9°50′N	37°41′E	1000	8–11 August 1968
Gughe (Mt), Gemu Gofa	6°05′N	37°20′E	2700	
Harar, Harar	9°20′N	42°08′E	2000	
Jiggigga Road (60 km E. of Harar)	9°14′N	42°32′E	1200	21–22 September 1968

Lake Abbaya, Gemu Gofa (S.W., near Arba Minch)	6°04′N	37°45′E	1300	6 August–3 September 1966
Lake Abbaya, Gemu Gofa (N.W., near Soddu)	6°40′N	38°00′E	1500	8–23 August 1964
Lake Chamo, Gemu Gofa (White Grasses)	5°58′N	37°55′E	1500	1966
Little Abbai, Gojjam	11°20′N	37°00′E	2000	27 August–5 September 1964
Mabil, Gojjam	10°19′N	36°45′E	900	14–20 August 1968
Mota, Gojjam	11°05′N	37°54′E	2500	
Metahara, Shoa	8°53′N	39°55′E	1000	
Mugher River (mouth of)	9°50′N	37°55′E	1000	8 August 1968
Nono, Upper Omo	8°30′N	37°21′E	1600	
Sabeta, Shoa	8°55′N	38°40′E	2500	
Shafartak	10°06′N	38°17′E	1150	
Sirba, Wollega	10°50′N	35°30′E	400	29–30 August 1968
Sire, Wollega	9°03′N	36°54′E	1800	
Soddu, Sidamo	6°45′N	37°50′E	1800	
Tississiat Falls	11°30′N	37°37′E	1800	
Valley of the Rocks, Harar	9°15′N	42°20′E	1300	21 September 1968
Wamet Ford	10°09′N	37°12′E	1000	20 August 1968

REFERENCES

Allen, G. M. 1939. A checklist of African mammals. *Bull. Mus. comp. Zool. Harv.* **83** : 1–763.

Anon. 1965. *The Royal Military Academy Expedition to Ethiopia, 1964: a report.*

—— 1967. *The Sandhurst Ethiopian Expedition 1966: a report.*

—— 1970. *The Great Abbai Expedition report 1968.* London: H.M.S.O.

Bate, D. M. A. 1947. An extinct reed-rat (*Thryonomys arkelli*) from the Sudan. *Ann. Mag. nat. Hist.* (11) **14** : 65–70.

—— 1949. The vertebrate fauna, in Arkell, A. J. *Early Khartoum.* Oxford.

Blashford-Snell, J. 1970. Conquest of the Blue Nile. *Geogr. J.* **136** : 42–60.

Blower, J. 1968. The wildlife of Ethiopia. *Oryx* **9** : 276–285.

Carcasson, R. H. 1964. A preliminary survey of the zoogeography of African butterflies. *E. Afr. Wildl. J.* **2** : 122–157.

Carpenter, G. D. H. 1935. The Rhopalocera of Abyssinia; a faunistic study. *Trans. R. ent. Soc. Lond.* **83** : 313–447.

Coetzee, C. G. 1967. Carnivora (excluding the family Felidae), in Meester, J. (ed.) *Preliminary identification manual for African mammals*, pt 7. Washington.

Corbet, G. B. & Hanks, J. 1968. A revision of the elephant-shrews, family Macroscelididae. *Bull. Br. Mus. nat. Hist. (Zool.)* **16** : 45–111, pl. 1.

Corbet, G. B. & Jones, L. E. 1965. The specific characters of the crested porcupines, subgenus *Hystrix*. *Proc. zool. Soc. Lond.* **144** : 285–300.

Cretzschmar, J. 1826. Säugethiere, in Rüppell, E. *Atlas zu der Reise in nordlichen Afrika.* Frankfurt am Main.

Davies, D. H. S. 1968. Rodentia, Gerbillinae: genera *Tatera* and *Gerbillurus*, in Meester, J. (ed.) *Preliminary identification manual for African mammals*, pt 18. Washington.

De Beaux, O. 1925. Mammiferi dell' Abissinia. *Atti. Soc. ital. Sci. nat.* **64** : 1–23.

—— 1930. Brevi note su alcuni mammiferi dell' Eritrea (*Arvicanthis, Lepus*). *Atti Soc. Sci. nat.* **69** : 1–5.

—— 1943. Mammalia, in *Missione biologica Sagan-Omo, VII, zoologia* **1** : 15–57. Rome.

DELANY, M. J. & NEAL, B. R. 1966. A review of the Muridae (Order Rodentia) of Uganda. *Bull. Br. Mus. nat. Hist.* (*Zool.*) **13** : 297–355.

DORST, J. & DANDELOT, P. 1970. *A field guide to the larger mammals of Africa.* London.

ELLERMAN, J. R. & MORRISON-SCOTT, T. C. S. 1951. *Checklist of Palaearctic and Indian mammals, 1758 to 1946.* London.

GLASS, B. P. 1965. The mammals of eastern Ethiopia. *Zool. Afr.* **1** : 177–179.

HAYMAN, R. W. 1960. Notes on some small African mammals. *Rev. Zool. Bot. afr.* **62** : 59–65.

—— 1966. On the affinities of *Nilopegamys plumbeus* Osgood. *Annls Mus. r. Afr. cent. Ser. 8°* **144** : 29–37.

HEIM DE BALSAC, H. & LAMOTTE, M. 1957. Evolution et phylogénie des Soricidés africaines. *Mammalia* **21** : 15.

HELLER, E. 1911. New species of rodents and carnivores from equatorial Africa. *Smithson. misc. Collns* **56** : (17) : 1–16.

HEUGLIN, M. T. VON. 1877. *Reise in Nordost-Afrika.* Braunschweig.

HILL, J. E. & MORRIS, P. 1971. Bats from Ethiopia collected by the Great Abbai Expedition 1968. *Bull. Br. Mus. nat. Hist.* (*Zool.*) **21** : 27–49, pl. 1–3.

INGERSOL, R. H. 1968. *The ecological significance of mammals in the eastern Chercher Highlands of Harar Province, Ethiopia.* Ph.D. thesis, Oklohoma State University.

KUMMER, H. 1968. Social organization of hamadryas baboons. *Biblithca primatol.* **6** : 1–189.

KUMMER, H., GOETZ, W. & ANGST, W. 1970. Cross-species modifications of social behaviour in baboons, in Napier, J. R. & Napier, P. H. (eds.) *Old world monkeys : evolution, systematics and behaviour.* New York & London.

LATASTE, F. 1886. Novi subgeneris et novae speciei rodentorum, e genere *Massoutiera. Naturaliste* **3** (8) : 287.

MATSCHIE, P. 1912. *Gazella* (*Nanger*) *soemmerringii sibyllae* subsp. nov. *Sber. Ges. naturf. Freunde Berl.* **1912** : 260–270.

MATTHEY, R. 1966. Cytogenetique et taxonomie des rats appartenent au sous-genre *Mastomys* Thomas (Rodentia, Muridae). *Mammalia* **30** : 105–119.

MISONNE, X. 1968. Rodentia: main text, in Meester, J. (ed.) *Preliminary identification manual for African mammals,* pt 19. Washington.

MOREAU, R. 1966. *The bird faunas of Africa and its islands.* London.

MORRISON-SCOTT, T. C. S. 1946. *Suncus etruscus* (Savi) in Africa. *Mammalia* **10** : 145.

NEUMANN, O. & RÜMMLER, H.–J. 1928. Beiträge zur Kenntnis von *Tachyoryctes* RÜPP. *Z. Säugetierk.* **3** : 295–306.

OSGOOD, W. H. 1936. New and imperfectly known small mammals from Africa. *Publ Field Mus. nat. Hist. Zool.* **20** : 217–256.

PETTER, F. 1959. Eléments d'une revision des lièvres africains du sous-genre *Lepus. Mammalia* **23** : 41–67.

—— 1963. Nouveaux eléments d'une revision des lièvres africains. *Mammalia* **27** : 238–255.

—— 1967. Lagomorpha, in Meester, J. (ed.) *Preliminary identification manual for African mammals,* pt 10. Washington.

PETTER, F. & CHIPPAUX, A. 1962. Description d'une musaraigne pygmée d'Afrique equatoriale, *Suncus infinitesimus ubanguiensis* subsp. nov. *Mammalia* **26** : 512–516.

POCOCK, R. I. 1944. Three races, one new, of the serval (*Leptailurus*) from North Africa. *Ann. Mag. nat. Hist.* (11) **11** : 690–698.

ROCHEBRUNE, A. T. 1883. Faune de la Sénegambie. *Acta Soc. linn. Bordeaux* (4) **7** : 49–204.

SCHWARZ, E. & SCHWARZ, H. K. 1967. A monograph of the *Rattus rattus* group. *An. Esc. nac. Cienc. biol. Mex.* **14** : 79–178.

SCOTT, H. 1958. Biogeographical research in High Simien (Northern Ethiopia), 1952–53. *Proc. Linn. Soc. Lond.* **170** : 1–91, pls. 1–17.

SETZER, H. W. 1956. Mammals of the Anglo-Egyptian Sudan. *Proc. U.S. Nat. Mus.* **106** : 447–587.

—— 1968. Rodentia, Muridae: genus *Acomys*, in Meester, J. (ed.) *Preliminary identification manual for African mammals*, pt 21. Washington.
SIMON, N. 1968. *Red data book, vol. 1, Mammalia.* Morges.
SNAILHAM, R. 1970. *The Blue Nile revealed.* London.
THOMAS, O. 1906. Description of new mammals from Mount Ruwenzori. *Ann. Mag. nat. Hist.* (7) **18** : 136–147.
—— 1928. Some rarities from Abyssinia with the description of a new mole-rat (*Tachyoryctes*) and a new *Arvicanthis*. *Ann. Mag. nat. Hist.* (10) **1** : 302–304.
URBAN, E. K. & BROWN, L. H. 1971. *A checklist of the birds of Ethiopia.* Addis Ababa.

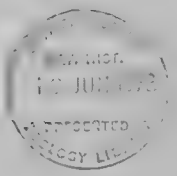
BRITISH MUSEUM
NAT. HIST.
19 JUN 1972
PRESENTED
ZOOLOGY LIBRARY

G. B. CORBET
Department of Zoology
BRITISH MUSEUM (NATURAL HISTORY)
CROMWELL ROAD
LONDON, SW7 5BD

D. W. YALDEN
Department of Zoology
UNIVERSITY OF MANCHESTER
MANCHESTER, M13 9PL

A LIST OF SUPPLEMENTS TO THE ZOOLOGICAL SERIES OF THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY)

1. KAY, E. ALISON. Marine Molluscs in the Cuming Collection British Museum (Natural History) described by William Harper Pease. Pp. 96; 14 Plates. 1965. (Out of Print.) £3.75.
2. WHITEHEAD, P. J. P. The Clupeoid Fishes described by Lacepede, Cuvier and Valenciennes. Pp. 180; 11 Plates, 15 Text-figures. 1967. £4.
3. TAYLOR, J. D., KENNEDY, W. J. & HALL, A. The Shell Structure and Mineralogy of the Bivalvia. Introduction. Nuculacea-Trigonacea. Pp. 125; 29 Plates 77 Text-figures. 1969. £4.50.
4. HAYNES, J. R. Cardigan Bay recent Foraminifera (Cruises of the R.V. *Antur*) 1962–1964. (*In Press*).



Printed in England by Staples Printers Limited at their Kettering, Northants, establishment

THE SHELL STRUCTURE AND MINERALOGY OF THE BIVALVIA

II. LUCINACEA – CLAVAGELLACEA CONCLUSIONS

J. D. TAYLOR

W. J. KENNEDY

A. HALL

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 22 No. 9

LONDON: 1973

THE SHELL STRUCTURE AND MINERALOGY OF THE BIVALVIA

II. LUCINACEA – CLAVAGELLACEA CONCLUSIONS

BY

JOHN DAVID TAYLOR

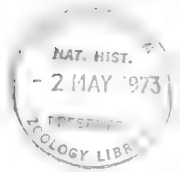
WILLIAM JAMES KENNEDY

Department of Geology & Mineralogy, University of Oxford

ANTHONY HALL

Department of Geology, Kings College, University of London

Pp. 253–294; *15 Plates, 33 Text-figures, 22 Tables*



BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 22 No. 9
LONDON : 1973

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 22, *No.* 9 *of the Zoological series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation
Bull. Br. Mus. nat. Hist. (Zool.).

© Trustees of the British Museum (Natural History), 1972

TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 16 *March*, 1973 *Price* £4·50

THE SHELL STRUCTURE AND MINERALOGY OF THE BIVALVIA

II. LUCINACEA — CLAVAGELLACEA CONCLUSIONS

By J. D. TAYLOR, W. J. KENNEDY & A. HALL

ABSTRACT

THE shell microstructure of twenty six remaining bivalve superfamilies is described with the aid of acetate peels and electronmicroscopy. In the order Heterodonta most shells consist of outer crossed-lamellar and an inner complex crossed-lamellar layers. Three superfamilies, the Lucinacea, Tellinacea and Veneracea have all, or some members, with an additional outer layer of composite prismatic structure. Minor variations consist of the occurrence of homogeneous structure in many families, resulting from a reduction in grain size and loss of crystal form in each structure. The order Myoida is more varied with crossed-lamellar and complex crossed-lamellar shells in the Corbulidae, Gastrochaenacea and some Pholadacea. The Hiatellacea are mainly all homogeneous but *Panopea* has a three layered shell consisting of an outer simple aragonite prismatic layer and middle and inner homogeneous layers. A very similar outer prismatic layer is found in some Pholadacea. In the Anomalodesmata two shell structure conditions are found, either a three layered shell, consisting of an outer layer of simple aragonite prisms and two nacreous layers or two homogeneous layers.

Twelve shell structure characters can be used as an aid to superfamilial classification; but they must be used in conjunction with other characters and geological history. The shell structure characters have been superimposed upon a phylogenetic tree derived from many characters; the points of variance and similarity of shell structure with this phylogeny are discussed in turn. It is suggested that the Arcoida may be more closely related to the Heterodonta than the Pteriomorphia. A 'pholadomyacean' stock has been in existence since the Ordovician and it is probable that both the Myoida and Anomalodesmata may be derived from this stock.

CONTENTS

	Page
INTRODUCTION	256
SYSTEMATIC DESCRIPTIONS	256
LUCINACEA	256
CHAMACEA	258
LEPTONACEA	259
CHLAMYDOCONCHACEA	259
CYAMIACEA	260
CARDITACEA	260
CRASSATELLACEA	261
CARDIACEA	263
TRIDACNACEA	264

CONTENTS—*Continued*

	Page
Mactracea	265
Solenacea	265
Tellinacea	266
Gaimardiacea	268
Arcticacea	268
Dreissenacea	268
Glossacea	269
Corbiculacea	269
Veneracea	270
Myacea	275
Gastrochaenacea	277
Hiatellacea	277
Pholadacea	279
Pholadomyacea	282
Pandoracea	282
Poromyacea	284
Clavagellacea	284
Conclusions	286
Acknowledgements	292
References	292

INTRODUCTION

This is the continuation to Taylor, Kennedy & Hall (1969) in which we reviewed Bivalve shell structure, mineralogy and shell formation, and documented these features in the superfamilies Nuculacea to Trigonacea. Here we describe the distribution of structures in the remaining superfamilies and discuss the importance of shell structures in the classification of the Class.

SYSTEMATIC DESCRIPTIONS

Since the publication of the first part of this work was published the Treatise of Invertebrate Palaeontology, Part N Bivalvia has appeared, which uses a system of classification slightly modified from that of Newell (1965) which we used previously. As the 'Treatise' classification will stand for some time we have used it for the arrangement of superfamilies described below.

Sub Class *HETERODONTA*

Order VENEROIDA

LUCINACEA

(Plate 1, figs 1, 2 & 5; Text-figs 1 & 2)

Fifteen species of this family have been examined mineralogically and ten structurally. The shell is aragonitic throughout.

Three main shell layers are present in all the species examined. There is an outer composite prismatic layer, a middle crossed-lamellar layer, which forms much of the hinge plate and an inner complex crossed-lamellar layer which is bounded by the

TABLE 1

LUCINACEA

Species	Locality	Mineralogy	Outer layer	Middle layer	Inner layer	Myostraca		Observations
						Pallial	Adductor	
Codakia punctata (Linnaeus)	Indo-Pacific	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	Thin bands of myostracal-type prisms and scattered large tubules in the inner layer
Codakia tigerina (Linnaeus)	Seychelles	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Thick prismatic	Prismatic	Myostracal-type prisms build the bulk of the inner layer

Species	Locality	Mineralogy	Outer layer	Middle layer	Inner layer	Myostraca		Observations
						Pallial	Adductor	

TABLE 1

LUCINACEA

Species	Locality	Mineralogy	Outer layer	Middle layer	Inner layer	Myostraca: Pallial	Myostraca: Adductor	Observations
Codakia punctata (Linnaeus)	Indo-Pacific	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	Thin bands of myostracal-type prisms and scattered large tubules in the inner layer
Codakia tigerina (Linnaeus)	Seychelles	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Thick prismatic	Prismatic	Myostracal-type prisms build the bulk of the inner layer, complex crossed-lamellar structure is best developed below the umbonal regions, where it contains fine bands of myostracal-type prisms and scattered tubules
Divaricella quadrisulcata (d'Orbigny)	W. Indies	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	Extensive layers of myostracal-type prisms in the inner layer. Tubules may be present
Fimbria lamellosa (Lamarck)	Eocene, Calcaire Grossier, France	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	Fine bands of myostracal-type prisms in the inner layer
Lucina columbella (Link)	Cape Verde	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Thick, prismatic	Not seen	Prominent layers of myostracal-type prisms in the inner layer
Lucina fijiensis Smith	Sarawak Borneo	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	Layers of myostracal-type prisms beneath umbo
Lucina pila Reeve	Oshima Japan	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Well-developed prismatic	Not seen	Extensive development of myostracal-type prisms in the inner layer
Lucina borealis (Linnaeus)	Galway	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	Extensive layer of myostracal-type prisms in the inner layer form the bulk of the marginal parts of this layer
Lucinopsis undata Forbes & Hanley	Tor Bay, England	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Well-developed, prismatic	Not seen	Extensive development of myostracal pillars in the inner layer
Corbis fimbriata Cuvier	East Indies	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	—	
Ctena divergens (Reeve)	Seychelles	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	—	
Divaricella eburnea (Reeve)	Ecuador	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	—	
Lonipes lucinalis (Link)	Malta	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic		
Lucinisca liana (Pilsbry)	Ecuador	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	—	
Thyasira sp.		Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	—	

Species	Locality	Mineralogy	Outer layer	Middle layer	Inner layer	Myostraca: Pallial	Myostraca: Adductor	Observations

trace of the pallial line. The outer composite prismatic layer is usually very thin but forms the ribs when present. The first order prisms lie with their long axes arranged radially to the umbo (Plate 1, fig. 1). In the middle crossed-lamellar layer the first order lamels are arranged with their long axes concentric to the shell margin. The lamels are often very fine when compared with some groups such as the Arcacea or Limopsacea but similar to those in the Carditacea and Astartacea. A prismatic pallial myostracum is present in all species examined, although variable in thickness. The inner shell layer is the most variable; complex crossed-lamellar structure is present in all species (Plate 1, figs 2 & 5) but varies in extent. The rest of the inner layer is made up of myostracal prisms which may occur as sheets, which alternate with the complex crossed-lamellar structure (*Lucina fijiensis*) or as large blocks (*Codakia tigerina*). These sheets of myostracal prisms may represent periods of temporary mantle attachment.

Scattered large tubules are present in the inner layer of *Codakia punctata*; tubules are also present in *Divaricella quadrisulcata* and *Codakia tigerina*.

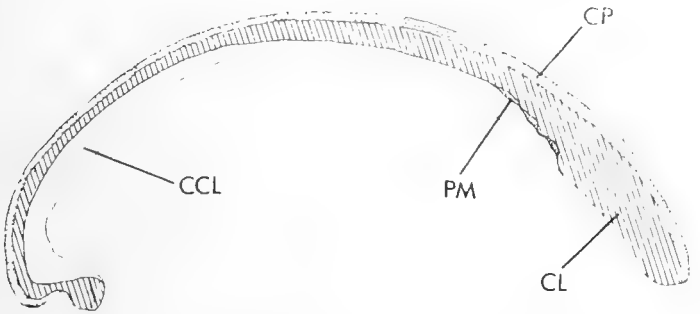


FIG. 1. Radial section of *Lucina columbella*. CP = composite prismatic, CL = crossed-lamellar, CCL = complex crossed-lamellar, PM = pallial myostracum.

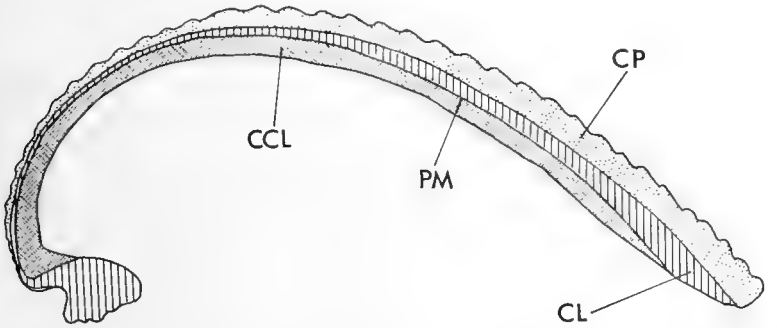


FIG. 2. Radial section of *Corbis fimbriata*. CP = composite prisms, CL = crossed-lamellar, CCL = complex crossed-lamellar, P = pallial myostracum.

CHAMACEA

(Text-fig. 3)

The shell structure, anatomy, and evolution of the Chamacea have been discussed in some detail elsewhere (Kennedy, Morris & Taylor, 1970), as has the shell structure and mineralogy of the anomalous species *Chama pellucida* (Taylor & Kennedy, 1969).

Amongst Recent species the shell is aragonitic throughout, with the exceptions of *Chama pellucida* and *C. exogyra*, which contain substantial amounts of calcite in a distinct outer layer. Two fossil species *Chama gryphina* (Miocene) and *Chama haueri* (Turonian) show traces of calcite but there is no evidence that this was an original feature of the shell.

In all wholly aragonitic species examined, two main shell layers are present (text-fig. 3). There is an outer, crossed-lamellar layer and an inner complex crossed-lamellar layer bounded by the trace of the pallial line. In the outer layer the first order lamels are arranged concentrically to the shell margin; in many specimens part of the outer layer may be missing apparently as a result of abrasion.

Myostraca are very well developed in the Chamacea, the pallial myostracum is thin, although always distinct and readily recognizable, extending throughout the hinge area. The adductor myostraca form thick pads and often interdigitate with the inner complex cross-lamellar layer as a result of slight shifting of attachment and body position during growth. In *Chama iostoma* other myostraca were seen presumably associated with the pedal muscles.

The inner shell layer of the Chamacea is basically formed of complex crossed-lamellar structure, varying from fine to coarse textured and complicated by sheets of myostracal type prisms and myostracal pillars. These features show varying development both inter and intra specifically. Myostracal pillars often arise from

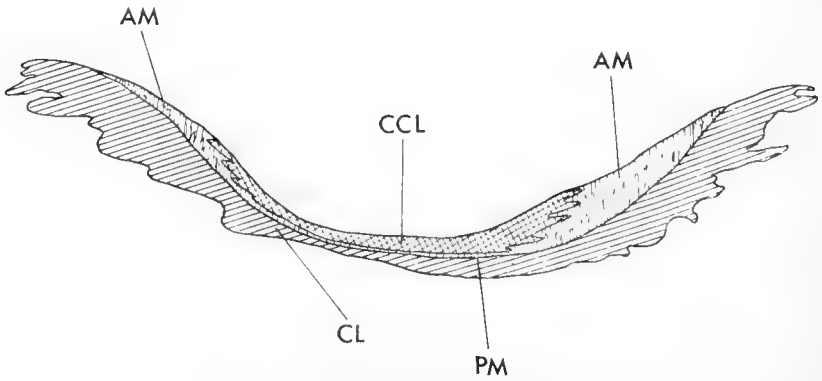


FIG. 3. Anterior-posterior section through *Pseudochama radians*. AM = adductor myostracum, PM = pallial myostracum, CL = crossed-lamellar, CCL = complex crossed-lamellar.

pallial and adductor myostraca. In *Chama spondyliodes* myostracal pillars are also present in parts of the outer crossed-lamellar layer. Seen on inner shell surface myostracal prisms are often arranged in rows radial from the umbo.

The Chamacea are markedly tubulate but there is much variation in the abundance and distribution of these structures which are usually confined to the inner layer.

Chama pellucida and *C. exogyra* differ from wholly aragonitic forms in possessing an outer prismatic calcite layer of unusual structure described by Taylor & Kennedy (1969). The remarkable occurrence of calcite was first noticed by Lowenstam (1954) but he considered (1964) that the outer crossed-lamellar layer of tropical species had changed to calcite prisms in the temperate *C. pellucida*. He used this example as evidence in the general temperature/mineralogy trends he demonstrated for invertebrate skeleta. However other temperate species of *Chama* seem to be wholly aragonitic.

A table of the shell structure characters of the thirty species of *Chama* examined will be found in Kennedy *et al* (1970, p. 390).

LEPTONACEA

Most species of this superfamily are very small and thin shelled. Four species were examined mineralogically and by electron-microscopy. The shell is aragonitic.

Two shell layers are present in all species examined; an outer crossed-lamellar layer and an inner complex crossed-lamellar layer. The two layers are separated by the prismatic pallial myostracum.

TABLE 2

LEPTONACEA

Species	Locality	Mineralogy	Outer layer	Inner layer	Pallial myostracum
Kellia suborbicularis Montagu	Britain	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Prismatic, thin
Kellia pustula Deshayes	Indian Ocean	Aragonite	Crossed-lamellar	Complex crossed-lamellar	
Scintilli oweni Deshayes	Karachi	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Prismatic, thin
Scintilla rosea Deshayes	Indian Ocean	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Prismatic, thin

CHLAMYDOCONCHACEA

Lack of material prevented examination of specimens of this peculiar monogeneric superfamily which have internal shells contained within mantle sacs.

CYAMIACEA

Three species of this small superfamily were examined structurally and mineralogically. In all three species the shell is aragonitic and consists of two layers both of them of fine granular homogeneous structure. The layers are separated by a thin prismatic pallial myostracum.

TABLE 3

CYAMIACEA

Species	Locality	Mineralogy	Outer layer	Inner layer	Pallial myostracum
Cyamium antarcticum (Philippi)	Falkland Islands	Aragonite	Homogeneous	Homogeneous	Prismatic
Cyamium laminiferum (Lamy)	Antarctic	Aragonite	Homogeneous	Homogeneous	Prismatic
Neodavisia cobbi (Cooper & Preston)	Falkland Islands	Aragonite	Homogeneous	Homogeneous	

CARDITACEA

(Plate 2, figs 4, 5 & 6; text-figs 4 & 5)

Fifteen species have been examined mineralogically and eleven structurally. The shell is aragonitic throughout.

Two main shell layers are present, an outer crossed-lamellar layer which forms the bulk of the hinge and teeth, and an inner complex crossed-lamellar layer which is bounded by the trace of the pallial myostracum. The first order lamels of the outer layer are very fine and are mostly arranged concentrically, but in some species a reflected shell margin causes the lamels to appear to have a radial alignment (Plate

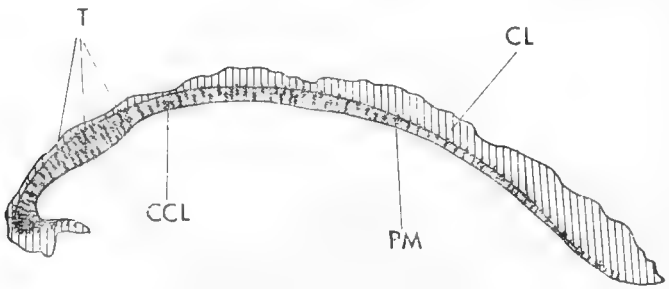


FIG. 4. Radial section of *Cardita variegata*. CL = crossed-lamellar, CCL = complex crossed-lamellar, PM = pallial myostracum, T = tubules.

TABLE 4

CARDITACEA

Species	Locality	Mineralogy	Outer layer	Inner layer	Myostraca		Observations
					Pallial	Adductor	
Cardita australis Lamarck	Auckland, New Zealand	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Not seen	Not seen	The crossed-lamellar layer is very fine. Fine tubules and prominent banding are present in the inner layer.
Cardita borealis	New England Dancray, France	Aragonite	Crossed-lamellar	Complex crossed-	Thin,	Not seen	The crossed-lamellar layer is banded, with abundant fine myostracal pillars, fine prismatic bands and fine tubules
Cardita aculeata Eichwald		Argonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	
Cardita sulcata Sowerby	Eocene, Britain	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	
Thecalia concamerata (de Blainville)	S. Africa	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	
Venericor planicostata (de Blainville)	Britain	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	

TABLE 4

CARDITACEA

Species	Locality	Mineralogy	Outer layer	Inner layer	Myostraca		Observations
					Pallial	Adductor	
Cardita australis Lamarck	Auckland, New Zealand	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Not seen	Not seen	The crossed-lamellar layer is very fine. Fine tubules and prominent banding are present in the inner layer.
Cardita borealis Conrad	New England	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	The crossed-lamellar layer is very fine, as is the complex crossed-lamellar layer. Fine tubules are present in the inner layer
Cardita calyculata Bruguière	Indian Ocean	Aragonite	Crossed-lamellar	Complex crossed-lamellar with myostracal pillars and bands of myostracal-type prisms	Thin, prismatic	Not seen	The crossed-lamellar layer is very fine, the complex-crossed lamellar layer has prominent banding, scattered, rather fine, myostracal layers and fine tubules
Cardita floridana Conrad	Florida	Aragonite	Crossed-lamellar	Crossed complex-lamellar	Thin, prismatic	Not seen	The structure of both layers is rather fine. There are abundant tubules in the inner layer
Cardita incrassata Sowerby	Queensland	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Not seen	Not seen	The structure of both layers is rather fine. There are fine tubules in the inner layer
Cardita marmorea Dunker	Queensland	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Not seen	Not seen	The structure of the crossed lamellar layer is rather fine. There are traces of fine prism layers and fine tubules in the inner layer
Cardita sowerbyi Deshayes		Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic?	Not seen	The structure of the crossed-lamellar layer is rather fine There are abundant myostracal pillars in the inner layer and a few in the marginal parts of the outer layer. Fine tubules are present in the inner layer
Cardita variegata (Bruguière)	Kenya	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	There are abundant myostracal pillars in the inner layer, and in the inner part of the outer layer where this lies below the inner layer. These pillars are also present throughout most of the outer layer outside the pallial line. Fine tubules in both layers
Carditamera affinis (Reeve)	Ecuador	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	The structure of the crossed-lamellar layer is rather fine. The inner layer is strikingly banded, with abundant fine tubules
Venericardia imbricata Lamarck	Calcaire Grossier, Lutetian, Dameray, France	Argaonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	The structure of the crossed-lamellet layer is rather fine. The inner layer is distinctly banded, with abundant fine myostracal pillars, fine prismatic bands and fine tubules
Cardita aculeata Eichwald		Argonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	
Cardita sulcata Sowerby	Eocene, Britain	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	
Thecalia concamerata (de Blainville)	S. Africa	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	
Venericor planicostata (de Blainville)	Britain	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	

TABLE 5

CRASSATELLACEA

Species	Locality	Mineralogy	Outer layer	Inner layer	Myostraca		Observations
					Pallial	Adductor	
Crassatella antillarum Reeve	W. Indies	Aragonite	Crossed-lamellar	Homogeneous	Indistinct, thin, prismatic?	Not seen	Outer layer very finely crossed-lamellar, inner layer with conspicuous banding
Crassatella decipiens Reeve	W. Australia	Aragonite	Crossed-lamellar	Homogeneous	Indistinct, thin,	Not seen	Outer layer very finely crossed-lamellar, inner layer
Conrad							
Astarte ellipta Macgillivray	Greenland	Aragonite					
Astarte quexii (d'Orbigny)	L. Lias, Blockley, Gloucs.	Aragonite					

Species	Locality	Mineralogy	Outer layer	Inner layer	Myostraca		Observations
					Pallial	Adductor	

TABLE 5

CRASSATELLACEA

Species	Locality	Mineralogy	Outer layer	Inner layer	Myostraca		Observations
					Pallial	Adductor	
Crassatella antillarum Reeve	W. Indies	Aragonite	Crossed-lamellar	Homogeneous	Indistinct, thin, prismatic?	Not seen	Outer layer very finely crossed-lamellar, inner layer with conspicuous banding
Crassatella decipiens Reeve	W. Australia	Aragonite	Crossed-lamellar	Homogeneous	Indistinct, thin, prismatic?	Not seen	Outer layer very finely crossed-lamellar, inner layer with conspicuous banding
Crassatella lamellosa Lamarck	Lutetian, Dameray, France	Aragonite	Crossed-lamellar	Homogeneous	Not seen	Not seen	Prominent banding in the inner layer
Crassatella radiata (Sowerby)		Aragonite	Crossed-lamellar	Homogeneous	Not seen	Not seen	
Eucrassatella gibbosa (Sowerby)	Ecuador	Aragonite	Crossed-lamellar	Homogeneous	Thin, prismatic	Thin, prismatic	Outer layer very finely crossed-lamellar, becoming homogeneous when traced inwards
Astarte borealis (Schumacher)	Greenland	Aragonite	Crossed-lamellar	Homogeneous with myostracal prisms	Thin, prismatic	—	Inner layer largely built of myostracal-type prisms, homogeneous structure present beneath umbones only
Astarte incrassata Deshayes	Pliocene, Italy	Aragonite	Crossed-lamellar	Complex crossed lamellar with myostracal prisms	Indistinct, thin, prismatic?	Not seen	Complex crossed-lamellar structure present only beneath umbones
Astarte obliqua Sowerby	Pliocene, Britain	Aragonite	Crossed-lamellar	Homogeneous with myostracal prisms	Thin, prismatic	Not seen	Myostracal-type prisms form most of the inner layer
Astarte omalii (Jonkiere)	Pliocene, Britain	Argonite	Crossed-lamellar	Complex crossed-lamellar with myostracal prisms	Indistinct, thin, prismatic	Not seen	Inner layer mostly built of myostracal-type prisms, inter-lingering with complex crossed lamellar structure in umbonal region
Astarte striata Sowerby	Greenland	Aragonite	Crossed-lamellar	Homogeneous with myostracal prisms	thin prismatic	—	Inner layer almost entirely built of myostracal-type prisms
Astarte sulcata (da Costa)	Pliocene, Italy	Aragonite	Crossed-lamellar	Complex crossed lamellar with myostracal prisms	Thin, prismatic	—	Inner layer almost entirely built of myostracal-type prisms
Astarte sulcata (da Costa)	Millport	Aragonite	Crossed-lamellar	Complex crossed-lamellar with myostracal prisms	Thin, prismatic	—	Inner layer almost entirely built of myostracal-type prisms
Crassatella dilatata Deshayes	Lutetian, Dameray, France	Aragonite					
Crassatella trigonata Lamarck	Lutetian, Dameray, France	Aragonite					
Crassinella lunatula Conrad	Florida	Aragonite					
Astarte ellipta Macgillivray	Greenland	Aragonite					
Astarte quexii (d'Orbigny)	L. Lias, Blockley, Glouc	Aragonite					

Species	Locality	Mineralogy	Outer layer	Inner layer	Myostraca		Observations
					Pallial	Adductor	

2, fig. 4). The outer layer is frequently very thin or worn off in the umbonal area.

A thin discontinuous prismatic pallial myostracum was seen in most species. In *Cardita calyculata* the prisms were seen in the umbonal area only.

The inner layer is somewhat variable; the complex crossed-lamellar structure is rather fine and prominent banding is seen in most species (Plate 2, fig. 6). Myostracal pillars are developed in several of the species examined: in *Cardita calyculata* and *Venericardia imbricata* they are restricted to the inner layer. In *C. sowerbyi* & *C. marmorea* there are abundant pillars in the inner layer and a few in the marginal parts of the outer layer (Plate 2, fig. 5). However in *C. variegata* there are abundant pillars in both inner and outer layers. Sheets of myostracal prisms are also present in the inner layer of *C. calyculata*, *C. marmorea* and *V. imbricata*.

Tubules are present in all the Carditacea examined and occur in the inner layer of all species and in both layers of *Cardita variegata*.

CRASSATELLACEA

(Plate 1, figs 3, 4, 6 & 8; Plate 2, figs 3 & 4; text-figs 6 & 7)

The superfamily Crassatellacea is represented by two living families, the Crassatellidae and the Astartidae Sixteen species have been examined mineralogically and twelve optically; the shell is aragonitic throughout.

In both families the shell consists of two layers; both have an outer crossed-lamellar layer but the inner layers differ. The inner layer of the Crassatellidae is homogeneous, whereas that of the Astartidae is largely built up of myostracal-type prisms, with only traces of complex crossed-lamellar or homogeneous structures. The outer crossed-lamellar layer of all the species examined is built up from very fine primary lamels, arranged concentrically with the shell margin (Plate 1, figs 3 & 4). The lamels are obvious in the outer parts of the layer but traced inwards they

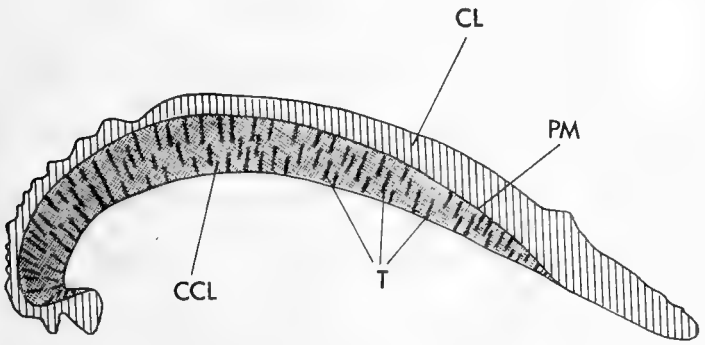


FIG. 5. Radial section of *Venericardia imbricata*. CL = crossed-lamellar, CCL = complex crossed-lamellar, PM = pallial myostracum, T = tubules.

become increasingly difficult to resolve and the layer appears homogeneous. Most of the hinge area is formed from crossed-lamellar structure.

The inner layer of the Crassatellidae shows no obvious macro-features other than conspicuous banding; electron-microscopy shows the structure to consist of irregular granular structure. In the Astartidae the inner layer is largely built up of myostracal prisms (Plate 1, figs 7 & 8; Plate 2, figs 2 & 3). In *Astarte borealis* scanning microscopy shows the outcropping prisms (Plate 2, fig. 3) revealed as distinct bosses; these show surface features of parallel ridges and striae. In *A. borealis* and *A. incrassata* there is a narrow homogeneous sheet on the inside of the pallial myostracum separating the myostracum from the main prismatic part of the inner layer. In other species the prisms arise directly from the pallial trace. There is considerable geometric selection of the prisms of the inner layer; those closest to the pallial myostracum are small and numerous but traced towards the inside of the shell there is a reduction in numbers and a resultant increase in size of the prisms.

The two shell layers are separated by the trace of the pallial myostracum. In the Crassatellidae this is marked by a distinct unconformity of growth lines but actual myostracal prisms have been detected in only one species. *Eucrassatella gibbosa* which is also the only species examined with a distinct prismatic layer associated with the adductor muscles. In the Astartidae all the species possess a prismatic myo-

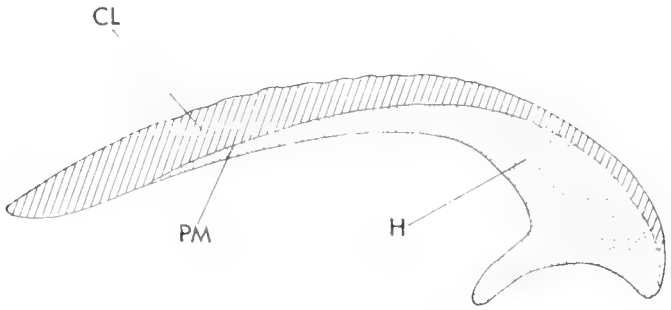


FIG. 6. Radial section of *Eucrassatella gibbosa*. CL = crossed-lamellar, H = homogeneous, PM = pallial myostracum.

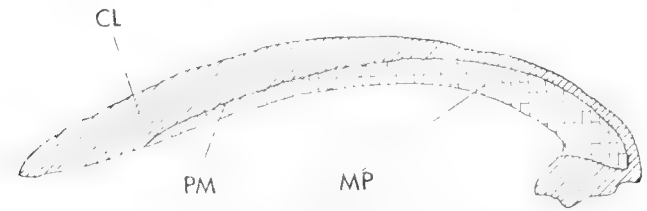


FIG. 7. Radial section of *Astarte borealis*. CL = crossed-lamellar, PM = pallial myo-stracum, MP = myostracal prisms.

TABLE 6

CARDIACEA

Species	Locality	Mineralogy	Outer layer	Inner layer	Myostraca		Observations
					Pallial	Adductor	
Acanthocardia aculeata	Britain France	Aragonite	Crossed-lamellar	Complex crossed-	Indistinct	Prismatic	
Parvicardium sueziense (Issel)	Seychelles	Aragonite					
Trachycardium senticosum (Sowerby)	Ecuador	Aragonite					

TABLE 6

CARDIACEA

Species	Locality	Mineralogy	Outer layer	Inner layer	Myostracum: Pallial	Myostracum: Adductor	Observations
Acanthocardia aculeata (Linnaeus)	Britain	Aragonite	Crossed lamellar	Complex crossed lamellar	Indistinct	Prismatic	
Acanthocardia echinata (Linnaeus)	Britain	Aragonite	Crossed lamellar	Complex crossed lamellar	Thin, prismatic	Prismatic	
Cerastoderma edule (Linnaeus)	Britain	Aragonite	Crossed lamellar	Complex crossed lamellar	Thin, prismatic	—	
Fragum unedo (Linnaeus)	China	Aragonite	Crossed-lamellar	Complex crossed lamellar	Thin, prismatic		
Hemicardia hemicardia (Linnaeus)	China	Aragonite	Crossed lamellar	Complex crossed-lamellar	Indistinct	—	
Laevicardium alternatum (Sowerby)		Aragonite	Crossed lamellar	Complex crossed-lamellar	Prismatic	—	Parts of the complex crossed-lamellar layer are in continuity with the first-order lamels of the outer layer
Laevicardium australe (Sowerby)	Seychelles	Aragonite	Crossed lamellar	Complex crossed lamellar	Indistinct		
Laevicardium crassum (Gmelin)	Dublin Bay	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	—	
Laevicardium serratum (Linnaeus)	Jamaica	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic		
Papyridea unguula (Sowerby)	Antilles	Aragonite	Crossed lamellar	Complex crossed-lamellar	Thin, prismatic	—	
Serripes groenlandicus (Moller)	Disco. Is Greenland	Aragonite	Crossed lamellar	Complex crossed lamellar	Prismatic	—	A thin-shelled form, fine crossed lamellar structure forms the hinge
Trachycardium consors (Sowerby)	Ecuador	Aragonite	Crossed lamellar	Complex crossed-lamellar	Thin, prismatic	—	Thin myostracal bands beneath umbo
Trachycardium maculosum (Wood)	Seychelles	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Indistinct		
Trigoniocardia guanocense (Hertlein & Strong)	Ecuador	Aragonite	Crossed-lamellar	Complex crossed lamellar	Prismatic	Prismatic	
Vasticardium incarnatum (Reeve)	Manilla	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic		
Acanthocardia parkinsoni (Sowerby)	Pleistocene, Britain	Aragonite					
'Cardium' ciliatum Fabricius	Greenland	Aragonite					
Loxocardium obliquum (Lamarck)	Lutetian, Damery, France	Aragonite					
Parvicardium suezense (Issel)	Seychelles	Aragonite					
Trachycardium senticosum (Sowerby)	Ecuador	Aragonite					

stracum beneath the pallial attachment, but no adductor myostracum was detected.

In a recent review of the Crassatellacea (Boyd & Newell 1968) a diphyletic origin for the superfamily was suggested. Our observations on the differences between the Crassatellidae and the Astartidae would tend to support this suggestion. The features of the Permian *Oriocrassatella elongata* described as "crater-like blisters in umbonal cavity" (Boyd & Newell, 1968) appear to be cavities left by the solution of myostracal prisms in the inner layer.

CARDIACEA

(Plate 3, figs 1–4; text-fig. 8)

Fifteen species of this group have been examined structurally and twenty mineralogically. The shell is aragonitic throughout.

Two main shell layers are present, an outer crossed-lamellar layer which forms the hinge and an inner complex crossed-lamellar layer which is bounded by the trace of the pallial line. In the outer layer the first order lamels are quite large and are aligned concentrically everywhere except for the hinge (Plate 3, figs 1, 2 & 3). Transverse sections show that the strong ribbing of most species of this superfamily produces complex patterns of first order lamels in the outermost part of the outer layer. This layer becomes very thin in the umbonal area and is frequently eroded and lost. There is a prismatic pallial myostracum in most Cardiacea, (indistinct in some species) which separates the inner complex crossed-lamellar layer. In *Laevicardium alternatum* the inner and outer layers are in direct local contact and the blocks of laths in each layer show structural continuity. Sections cut through the adductor muscle scars of some species show lenses of myostracal prisms. Bands of myostracal prisms associated with pedal muscles were seen in the umbonal area of *Trachycardium consors*.

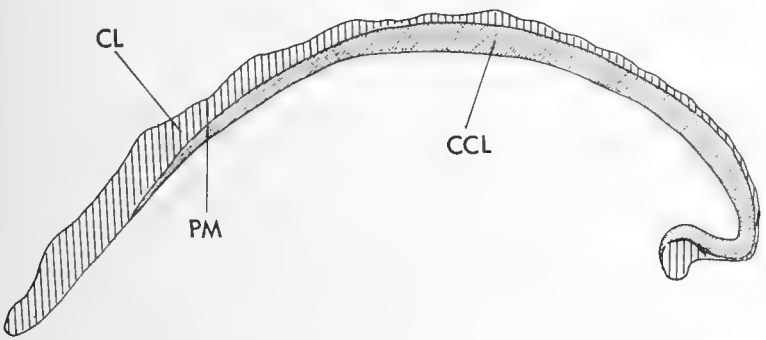


FIG. 8. Radial section of *Cerastoderma edule*. CL = crossed-lamellar, PM = pallial myostracum, CCL = complex crossed-lamellar.

TRIDACNACEA

(Plate 3, figs 5–8; text-fig. 9)

This is a small superfamily closely related to the Cardiacea (Stasek, 1962); included genera are *Tridacna* and *Hippopus*. Four species have been examined structurally and mineralogically. The shell is wholly aragonitic.

The shell is very thick, with two shell layers, an outer crossed-lamellar layer and an inner complex crossed-lamellar layer which is bounded in extent by the trace of the pallial line. In the outer layer the first order lamels are large (Plate 3, fig. 6) and arranged concentrically in all but the hinge area. The strong ribbing however causes an apparent complex pattern of first order lamels (Plate 3, fig. 4). There is a thin prismatic pallial myostracum in all the species examined. The inner complex crossed-lamellar layer is somewhat variable in character; in the three species of *Tridacna* studied the structural elements are fairly coarse and interleaved with thin sheets of myostracal-prisms. In *Hippopus* however the structure is very fine with an almost homogeneous appearance and with many fine prismatic sheets (Plate 3, figs 7 & 8). Higher magnifications (Plate 3, fig. 7) show that the structure consists of sheets of fine needles.

All species show very strong daily growth bands in both layers and show prismatic pedal and adductor myostraca.

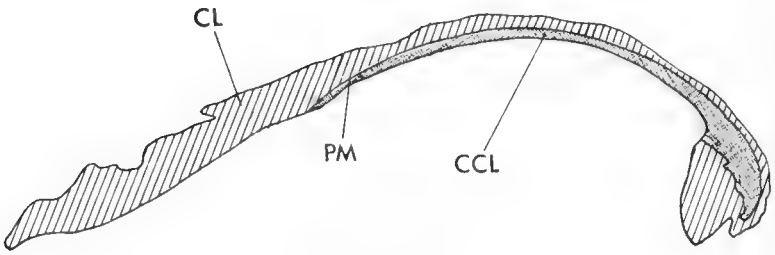


FIG. 9. Radial section of *Tridacna maxima*. CL = crossed-lamellar, CCL complex crossed-lamellar, PM = pallial myostracum.

TABLE 7

TRIDACNACEA

Species	Locality	Mineralogy	Outer layer	Inner layer	Myostraca		Observations
					Pallial	Adductor	
Hippopus hippopus Linnaeus	Australia	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Thin, prismatic	Prism bands in inner layer
Tridacna crocea Lamarck	East Indies	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Thin, prismatic	Prism bands in inner layer, pedal myostraca
Tridacna maxima Röding	Indian Ocean	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Thin, prismatic	Prism bands in inner layer, pedal myostraca

Name	Locality	Mineralogy	Outer layer	Inner layer	Myostraca		Observations
					Pallial	Adductor	
Ensis ensis (Linnaeus)	Britain	Aragonite	Finely crossed-lamellar	Homogeneous, lamellate	Thin, prismatic	—	
Ensis siliqua (Linnaens)	Britain	Aragonite	Finely crossed-lamellar	Homogeneous, lamellate	Thin, prismatic	—	
Cultellus lactuosus (Spengler)	India	Aragonite	Finely crossed-lamellar to homogeneous	Homogeneous, lamellate	Thin, prismatic	—	
Siliqua sp.	Ecuador	Aragonite	Finely crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	—	
Solen truncata (Wood)	Ceylon	Aragonite					

TABLE 7

TRIDACNACEA

Species	Locality	Mineralogy	Outer Layer	Inner Layer	Myostraca		Observations
					Pallial	Adductor	
Hippopus hippopus Linnaeus	Australia	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Thin, prismatic	Prism bands in inner layer
Tridacna crocea Lamarck	East Indies	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Thin, prismatic	Prism bands in inner layer, pedal myostraca
Tridacna maxima Röding	Indian Ocean	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Thin, prismatic	Prism bands in inner layer, pedal myostraca
Tridacna squamosa Lamarck	Indian Ocean	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Thin, prismatic	Prism bands in inner layer, pedal myostraca

TABLE 8

MACTRACEA

Name	Locality	Mineralogy	Outer Layer	Inner Layer	Myostraca		Observations
					Pallial	Adductor	
Atactodea glabrata (Gmelin)	Seychelles	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	
Mactra corallina (Linnaeus)	Britain	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Not seen	Not seen	
Mactra leucozonica Philippi	Philippines	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Not seen	Not seen	
Mactra producta Angas	Port Jackson	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Indistinct, prismatic	Indistinct, prismatic	
Mactra violacea Solander	Tranquebar	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Thin, prismatic	
Matronella elisea Dall	Ecuador	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	
Mactronella exoleta (Gray)	W. America	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	
Mulina pallida Broderip & Sowerby	Ecuador	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	Thin bands of myostracal-type prisms in the inner layer
Raeta undulata (Gould)	Ecuador	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Thin, prismatic	Thin bands of myostracal-type prisms in the inner layer
Spisula solida (Linnaeus)	Britain	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	Inner layer very fine, with sheets of myostracal-type prisms. Pedal myostraca visible beneath umbo
Cardilia martini (Deshayes)	Indian Ocean	Aragonite					
Mactroderma velata Philippi	Ecuador	Aragonite					

TABLE 9

SOLENACEA

Name	Locality	Mineralogy	Outer Layer	Inner Layer	Myostraca		Observations
					Pallial	Adductor	
Ensis ensis (Linnaeus)	Britain	Aragonite	Finely crossed-lamellar	Homogeneous, lamellate	Thin, prismatic	—	
Ensis siliqua (Linnaeus)	Britain	Aragonite	Finely crossed-lamellar	Homogeneous, lamellate	Thin, prismatic	—	
Cultellus lactuosus (Spengler)	India	Aragonite	Finely crossed-lamellar to homogeneous	Homogeneous, lamellate	Thin, prismatic	—	
Siliqua sp.	Ecuador	Aragonite	Finely crossed-lamellar	Crossed-lamellar	Thin, prismatic		
Solen truncata (Wood)	Ceylon	Aragonite					

MACTRACEA

(Plate 4, figs 1 & 2; text-fig. 10)

Thirteen species have been examined mineralogically and ten structurally. The shell is entirely aragonite.

There are two shell layers in all species examined, an outer crossed-lamellar layer and an inner complex crossed-lamellar layer bounded by the pallial myostracum. In the outer layer, the first order lamels are arranged concentrically and in this superfamily are characteristically very fine (Plate 4, fig. 2). The layer is usually very thin and worn in the umbonal region but forms most of the hinge. In *Spisula solida* the crossed-lamellae are finer than in most other species and appear homogeneous in the inner parts of the layer. The inner layer of this species also has a very fine structure and sheets of myostracal prisms are present. These sheets also occur in *Raeta undulata*. The separation of the two layers is sharp (Plate 4, fig. 1) but the pallial myostracum is thin and indistinct in most species. The adductor myostraca are also poorly defined.

SOLENACEA

(Plate 4, fig. 3)

Seven species have been examined mineralogically and four structurally. The shell is aragonitic throughout. Two main shell layers are present, an outer crossed-lamellar layer which forms the hinge and an inner homogeneous layer bounded by the trace of the pallial line. In the outer crossed-lamellar layer the first order lamels are very fine and arranged concentrically to the shell margin over most of the shell. Locally this layer may appear homogeneous. A very thin prismatic pallial myostracum, best developed below the umbo is present in all species. The inner layer of all the examples appears homogeneous with a striking lamellate appearance. Electron-microscopy of the inner layer of *Ensis siliqua* shows that the apparent homogeneous layer is in fact built up from layers of very fine complex crossed-lamellar structure (Plate 4, fig. 3) which alternate with bands of fibrous appearance which may be organic matrix. Etching reveals the presence of a reticulum of organic matrix sandwiched between carbonate laths.

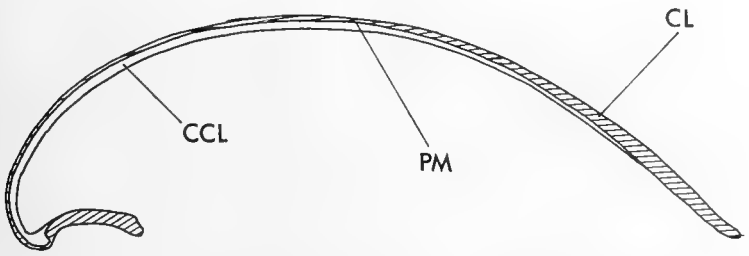


FIG. 10. Radial section of *Mactronella exoleta*. CL = crossed-lamellar, CCL = complex crossed-lamellar, PM = pallial myostracum.

TELLINACEA

(Plate 4, figs 4, 5 & 6; Plate 5, figs 1–7; Text-figs 11–15)

Thirty-one species have been examined mineralogically and twenty-four optically. The shell is totally aragonite.

Most of the species we have examined have three layered shells (Plate 4, fig. 4), with an outer composite prismatic layer, a middle crossed-lamellar layer and an inner layer which may be made of complex crossed-lamellar or homogeneous structures. The inner layer is, as usual, bounded by the pallial trace. In *Egeria radiata*, *Florimetis corrugata*, *Psammotea radiata*, *Macoma balthica*, *Tellidora burneti* and two species of *Solenotellina*, there are however only two shell layers, an outer crossed-lamellar layer and an inner, complex crossed-lamellar layer which is bounded by the trace of the pallial line. Trueman (1942) described a three layered shell in *Tellina tenuis*.

The outer composite prismatic layer of three layered species is usually very thin and is frequently worn away from the umbonal area. It consists of horizontal first order prisms, arranged radially from the umbo. Each prism is built up of fine needle-like second order prisms (Plate 4, figs 5 & 6) which are arranged in the characteristic divergent feathery pattern seen in longitudinal section. This layer is at its thickest development in the Donacidae and Semelidae, where the arrangement of first and second order prisms is very clear. The Donacidae develop strong internal marginal denticles with a resultant thickening of the outer shell layer (as in the Nuculidae).

The middle layer of three layered shells and the outer layer of two layered shells is built of crossed-lamellar structure with rather fine concentrically arranged first order lamels (Plate 4, fig. 4; Plate 5, fig. 3). This layer forms the hinge in all species examined.

The inner layer of most species examined is built of complex crossed-lamellar structure (Plate 5, figs 5 & 6) although as in the Solenacea the fabric is so fine as to appear homogeneous under light microscopy (Plate 5, fig. 7). Electron-microscopy reveals that this is very fine complex crossed-lamellar structure. In some species *Quidnipagus palatam*, *Asaphis deflorata*, and *Psammotea radiata* thin prismatic sheets are developed. In *Semele tortuosa* these occupy most of the inner layer (Plate 5, figs 1 & 2). The inner layer is also often markedly lamellate caused by the presence of thick sheets of protein matrix which presumably account for the flexibility of these shells.

Most species possess a thin prismatic pallial myostracum (Plate 5, fig. 2) although this may be indistinct in some and marked only by a sharp break in growth lines. Sections through adductor muscle scars reveal pads of myostracal prisms whilst thin prismatic bands of the trace pedal muscle attachment were seen beneath the hinge line in *Psammotea occidens*, *Solenotellina diphos*, and *Tellina calcarina*.

A 'so called' new shell layer called the mosaicostracum has been recognized in the Tellinacea on the basis of surface morphology by Hamilton (1969). We are uncertain how this relates to the layers recognized herein.

We have examined the fine structure of *Semele tortuosa*, *Donax faba*, *hecuba scortum*, *Tellina radiata*, *Quidnipagus palatam*, *Asaphis deflorata* and *Scutarcopagia scobinata*.

TABLE 10

TELLINACEA

Name	Locality	Mineralogy	Outer layer	Middle layer	Inner layer	Myostraca		Observations
						Pallial	Adductor	
Asaphis deflorata (Linnaeus)	Seychelles	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Prismatic	Prismatic	Inner layer fine, banded
Donax asper Hanley	Ecuador	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Prismatic	—	
Donax epidermia Lamarck	Brisbane	Aragonite	Composite prismatic	Crossed-lamellar	Homogeneous/ complex crossed-lamellar	Prismatic	—	Inner layer lamellate
Tellinella virgata Linnaeus	Indian Ocean	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Prismatic	—	Inner layer lamellate
Tellidora burneti (Broderip & Sowerby)	Mazaltan	Aragonite	Crossed-		Homogeneous	—	—	Inner layer lamellate

The following species are all aragonitic:—

Donax denticulatus Linnaeus	W. Indies
Donax transversus Sowerby	Ecuador
Gastrana fragilis (Linnaeus)	Italy
Scissulina dispar (Conrad)	Seychelles
Solecurtus broggi Pilsbry & Olsson	Ecuador
Strigilla carinaria (Linnaeus)	Ecuador

TABLE 10

TELLINACEA

Name	Locality	Mineralogy	Outer layer	Middle layer	Inner layer	Myostraca		Observations
						Pallial	Adductor	
Asaphis deflorata (Linnaeus)	Seychelles	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Prismatic	Prismatic	Inner layer fine, banded
Donax asper Hanley	Ecuador	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Prismatic	—	
Donax cyclicus Lamarck	Brisbane	Aragonite	Composite prismatic	Crossed-lamellar	Homogeneous complex crossed-lamellar	Prismatic		Inner layer lamellate
Donax faba Gmelin	Swan River, Australia	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Prismatic	—	
Donax vittatus (da Costa)	Britain	Aragonite	Composite prismatic	Crossed-lamellar	Homogeneous complex crossed-lamellar	Prismatic		Inner layer lamellate
Egeria radiata (Lamarck)	S. Nigeria	Aragonite	Crossed-lamellar		Complex crossed-lamellar	Prismatic	—	
Florimetis corrugata (Sowerby)	Ecuador	Aragonite	Crossed-lamellar		Complex crossed-lamellar	Prismatic		Tubules? in inner layer
Hecuba scortum (Linnaeus)	S. Africa	Aragonite	Composite prismatic	Crossed-lamellar	Homogeneous			Lamellate inner layer
Macoma balthica (Linnaeus)	Britain	Aragonite	Crossed-lamellar	—	Complex crossed-lamellar	Prismatic	—	
Psammotea occidens Deshayes	Philippines	Aragonite	Composite prismatic	Crossed-lamellar	Homogeneous	Prismatic	—	Inner layer lamellate
Psammotea radiata (Philippi)	Seychelles	Aragonite	Crossed-lamellar	—	Complex crossed-lamellar	Prismatic	—	Prism bands in inner layer
Quadrapagas pilsbryi Iredale	Seychelles	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Prismatic	—	
Scadicularia magna (Sprengler)	Ecuador	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Prismatic		
Scadrae paga linguafelis (Linnaeus)	Antilles	Aragonite	Composite prismatic	Crossed	Homogeneous			Inner layer lamellate
Scadrae paga sulcata (Linnaeus)	Queensland	Aragonite	Composite prismatic	Crossed-lamellar	Homogeneous			Inner layer lamellate
Semele bellastriata (C. B. Adams)	Ecuador	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Prismatic	—	Very thick pallial myostracum
Semele sp	Ecuador	Aragonite	Composite prismatic	Crossed-lamellar	Homogeneous			Lamellate inner layer
Solecurtus strigilatus Blainville	Mediterranean	Composite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar			Inner layer lamellate
Solenidellina capsoides (Sowerby)	India	Aragonite	Crossed-lamellar		Complex crossed-lamellar	Prismatic		Thin prism bands in inner layer, broad myostracum beneath umbo
Solecurtus broadbenti (Wood)	Swan River, Australia	Aragonite	Crossed-lamellar		Complex crossed-lamellar	Prismatic	Prismatic	Inner layer lamellate
Macoma calcarea (Gmelin)	Greenland	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Prismatic		Prism bands present in inner layer beneath hinge
Tellina radiata Linnaeus	W. Indies	Aragonite	Composite prismatic	Crossed-lamellar	Homogeneous			Inner layer lamellate
Tellina scobinata Linnaeus	Indian Ocean	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Prismatic		Inner layer lamellate
Tellidora burneti (Broderip & Sowerby)	Mazatlan	Aragonite	Crossed-lamellar		Homogeneous			Inner layer lamellate

The following species are all aragonitic:—

Donax denticulatus Linnaeus	W. Indies
Donax trifasciatus Sowerby	Ecuador
Gastrana fragilis (Linnaeus)	Italy
Scissulina dispar (Gmelin)	Seychelles
Solecurtus broggi Pilsbry & Olsson	Ecuador
Strigilla flexuosa (Linnaeus)	Ecuador

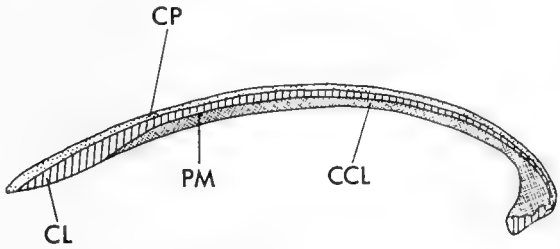


FIG. 11. Radial section of *Donax faba*. CP = composite prismatic, CL = crossed-lamellar, CCL = complex crossed-lamellar, PM = pallial myostracum.

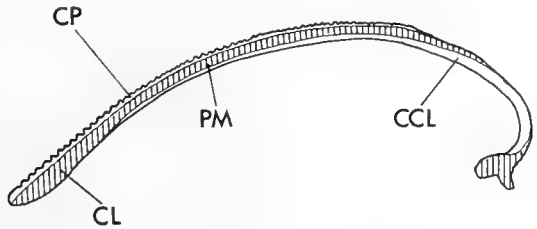


FIG. 12. Radial section of *Hecuba scortum*. CP = composite prismatic, CL = crossed-lamellar, PM = pallial myostracum, CCL = complex crossed- lamellar.

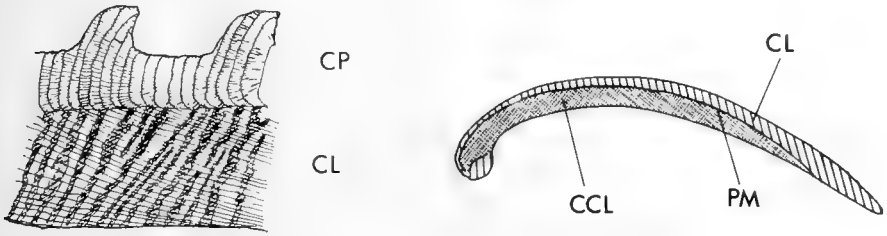


FIG. 13. Detail of a radial section of *Hecuba scortum* showing alignment of crystallites in the outer composite prismatic layer (CP), and of lamellae in the middle crossed-lamellar layer (CL).

FIG. 14. Radial section of *Macoma balthica*. CL = crossed-lamellar, CCL = complex crossed-lamellar, PM = pallial myostracum.

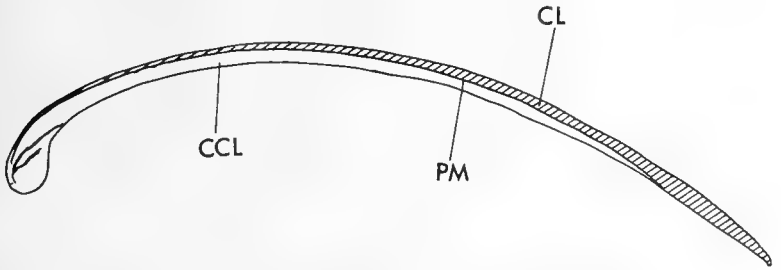


FIG. 15. Radial section of *Solenotellina sipho*. CL = crossed-lamellar, CCL = complex crossed-lamellar, PM = pallial myostracum.

GAIMARDIACEA

(Plate 6, figs 5 & 6)

Only one species was examined from this small superfamily, it is aragonitic. *Gaimardia trapezina* (Lamarck) from Tierra del Fuego has a two layered shell. Both layers are made up of homogenous structure; the constituent crystallites are very small about 0·5 μ in diameter and have irregular rounded outlines so that the structure appears granular (Plate 6, figs 5 & 6). The two layers are separated by a thin prismatic pallial myostracum.

ARTICACEA

Four species of this group have been examined structurally and six mineralogically. The shell is entirely aragonitic but there is some variation of structure within the superfamily.

In *Trapezium* and *Coralliophaga* there is an outer crossed-lamellar layer and an inner complex crossed-lamellar layer bounded by the trace of the pallial line. The primary lamels of the outer layer are very coarse and are arranged concentrically to the shell margin; this layer also forms the hinge. There is a thin prismatic pallial myostracum dividing the layers.

In *Arctica islandica* there are two shell layers, but in contrast to the other members of the family, both layers are built of homogeneous structure. The two layers are separated by an extremely fine prismatic pallial myostracum along which there is a distinct break in growth lines and shell layering. Details of the fine structure of the homogeneous structure were given in Taylor *et al* (1969).

A specimen of *Calyptogena ponderosa*, a member of the problematical family the Vesicomyidae was examined. Members of this family exhibit certain similarities with both the Veneracea and the Arcticacea, Boss (1968). The shell structure consists of two homogeneous layers and in this respect resembles the Arcticacea more than any other superfamily and is thus placed here for convenience. A similar conclusion was reached by Oberling & Boss (1970).

DREISSENACEA

(Plate 6, fig. 3; Text-fig. 16)

This is a small group of byssate freshwater bivalves of which we have examined one species structurally and three mineralogically The shell is aragonitic.

In *Dreissena polymorpha* an outer crossed-lamellar layer (Plate 6, fig. 3) and an inner complex crossed-lamellar layer are present; the former forms most of the hinge. The layers are separated by a thin prismatic pallial myostracum. The primary lamels of the outer layer are arranged concentrically.

TABLE II

ARCTICACEA

Name	Locality	Mineralogy	Outer layer	Inner layer	Myostraca		Observations
					Pallial	Adductor	
Coralliophaga coralliophaga (Gmelin)	Mollucas	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Prismatic	—	
Trapezium oblongum (Linnaeus)	Indian Ocean	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Prismatic	—	
Calyptogena ponderosa Boss	G. of Mexico	Aragonite	Homogeneous	Homogeneous		—	
Arctica islandica (Linnaeus)	Britain	Aragonite	Homogeneous	Homogeneous	Thin, prismatic	Indistinct	Thin prismatic bands in inner layer. Prominently banded
Corbicula occidens Deshayes	India	Aragonite	Finely crossed-lamellar	Complex-crossed-lamellar	Indistinct	—	very regular columns, as in the Limopsacea
Corbicula sp.	Lake Nyanza	Aragonite	Finely crossed-lamellar	Complex crossed-lamellar	Indistinct	—	Inner layer as above
Cyrena inflata Say	Nicaragua	Aragonite	Finely crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	—	Inner layer as above
Polymesoda anomala (Deshayes)	Ecuador	Aragonite	Finely crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	—	The pallial myostracum is discontinuous
Velorita cyprinoides (Gray)	Mangalore, India	Aragonite	Finely crossed-lamellar	Complex crossed-lamellar	Indistinct	—	Thin sheets of myostracal-type prisms are present in the inner layer
Corbicula cordata (Morris)	Sparnacian, Britain	Aragonite					Inner layer as in *C. fluminea*
Corbicula cuneiformis (Sowerby)	Sparnacian, Britain	Argonite					
Cyrena consobrina (Cailliaud)		Aragonite					
Pisidium amnicum Müller	Notts., England	Aragonite					

TABLE 11

ARCTICACEA

Name	Locality	Mineralogy	Outer layer	Inner layer	Myostraca		Observations
					Pallial	Adductor	
Coralliophaga coralliophaga (Gmelin)	Mollucas	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Prismatic	—	
Trapezium oblongum (Linnaeus)	Indian Ocean	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Prismatic		
Calyptogena pondersa Boss	G. of Mexico	Aragonite	Homogeneous	Homogeneous		—	
Arctica islandica (Linnaeus)	Britain	Aragonite	Homogeneous	Homogeneous	Thin, prismatic	Indistinct	Thin prismatic bands in inner layer Prominently banded
Arctica plana (Sowerby)	Tertiary, Thanetian, Britain	Aragonite					
Arctica cordiformis (Sowerby)	Cretaceous, Albian, Britain	Aragonite					

TABLE 12

DREISSENACEA

Species	Locality	Mineralogy	Outer layer	Inner layer	Myostraca		Observations
					Pallial	Adductor	
Dreissena polymorpha (Pallas)	Notts., England	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin prismatic		Outer layer forms fringe
Dreissena polymorpha (Pallas)	Bessarabia	Aragonite					
Dreissena africana van Beneden	Nigeria	Aragonite					
Dreissena brandi	Eocene, Britain	Aragonite					

TABLE 13

GLOSSACEA

Species	Locality	Mineralogy	Outer layer	Inner layer	Myostraca		Observations
					Pallial	Adductor	
Glossus humanus (Linnaeus)	Isle of Man	Aragonite	Homogeneous	Complex crossed-lamellar with bands of myostracal type prisms	Thin, prismatic	Thin, prismatic	Many prism bands in inner layer
Glossus humanus (Linnaeus)	Pleistocene Italy	Aragonite	Homogeneous	Complex crossed-lamellar with bands of myostracal type prisms	Thin, prismatic	Thin, prismatic	Prism bands in inner layer
Microcardia lamellata (Reeve)	Japan	Aragonite	Crossed-lamellar	Complex crossed-lamellar structure	Thin, prismatic		

TABLE 14

CORBICULACEA

Species	Locality	Mineralogy	Outer layer	Inner layer	Myostraca		Observations
					Pallial	Adductor	
Corbicula fluminea (Lamarck)	Japan	Aragonite	Finely crossed-lamellar	Complex crossed-lamellar	Indistinct		The complex crossed-lamellar layer shows laths arranged in very regular columns, as in the [illegible]
Corbicula cor[illegible] Deshayes	India	Aragonite	Finely crossed-lamellar	Complex-crossed-lamellar	Indistinct	—	Inner layer as above
Corbicula sp.	Lake Nyanza	Aragonite	Finely crossed-lamellar	Complex crossed-lamellar	Indistinct	—	Inner layer as above
Cyrena inflata Say	Nicaragua	Aragonite	Finely crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	—	The pallial myostracum is [illegible]
Pisidium diaphanum Deshayes	Ecuador	Aragonite	Finely crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	—	Thin sheets of myostracal-type prisms are present in the inner layer
Corbicula cyprinoides (Gray)	Madagascar, India	Aragonite	Finely crossed-lamellar	Complex crossed-lamellar	Indistinct	—	Inner layer as in *C. fluminea*
Corbicula cordata (Morris)	Sparnacian, Britain	Aragonite					
Corbicula consobrina (Sowerby)	Sparnacian, Britain	Aragonite					
Cyrena consobrina (Calhaud)		Aragonite					
Pisidium amnicum Müller	Notts., England	Aragonite					

GLOSSACEA

(Plate 6, fig. 1)

Two species of this very small superfamily have been examined structurally and mineralogically. The shell consists of aragonite.

In *Glossus humanus* there is an outer layer which is largely homogeneous and an inner complex crossed-lamellar layer which is bounded by the trace of the pallial line. In some specimens and in some parts of the shell there is a faint vertical structure similar to crossed-lamellar structure (Plate 6, fig. 1). The inner layer is built of rather fine lamels and in all specimens there are many thin sheets of myostracal prisms. In very old individuals where the inner layer is thick these prism sheets become abundant and closely spaced; in some irregularities develop and spherulite patterns appear in some sections. This is probably due to the development of corrugations upon the accretionary surface.

In *Meiocardia lamarckii* there is an outer crossed-lamellar layer in which the lamels are distinct and arranged concentrically; within this there is an inner complex crossed-lamellar layer bounded by a thin prismatic pallial myostracum.

CORBICULACEA

(Plate 6, figs 2 & 4)

Six species of this superfamily have been examined structurally and ten mineralogically. The shell is totally aragonite.

Again two shell layers are present, an outer crossed-lamellar layer which forms the hinge and teeth and an inner complex crossed-lamellar layer bounded by the trace of the pallial line. In the outer layer the lamels are rather fine and arranged concentrically (Plate 6, fig. 4). In most forms no prismatic pallial myostracum is visible only a dense granular zone separating the layers. Prisms are however detectable in *Polymesoda* and *Velorita cyprinoides*. The inner complex crossed-lamellar layer is always built of rather coarse laths, and in all species of *Corbicula* examined and in *Velorita* these are arranged in columns as in the Limopascea (Taylor *et al*, 1969). Tubules were seen in *Pisidium amnicum*.

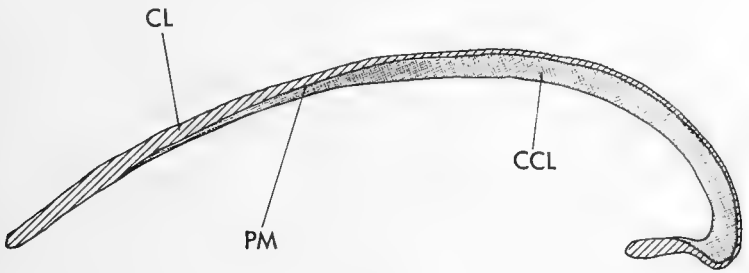


FIG. 16. Radial section of *Dreissena polymorpha*. CL = crossed-lamellar, CCL = complex crossed-lamellar, PM = pallial myostracum.

VENERACEA

(Plate 7, figs 1–5; Plate 8, figs 1–5; Text-figs 17–22)

This superfamily includes a large number of extant genera and species, consequently we have examined over fifty species structurally and mineralogically. The shell is aragonitic in all species. Both Boggild (1930) and Oberling (1964) stated that the distribution of shell structure types is highly variable, thus in order to ascertain if there is any systematic variation we have listed and discussed the species examined at family and sub-family level. (Table 15).

The shell structural variations found are indeed more variable than any other superfamily. The various combinations are shown diagrammatically in Text-fig. 17. The apparently most important structural distinction is that between species having an outer composite prismatic layer and those without. The other variations exhibited between crossed-lamellar, complex crossed-lamellar and homogeneous structures almost always show transitions and all gradations between these structures may be found.

There is thus in many species a basically three layered shell consisting of an outer composite prismatic layer, a middle crossed-lamellar/homogeneous layer and an inner complex crossed-lamellar/homogeneous layer. In most other species the shell is basically two layered with an outer crossed-lamellar/homogenous layer and an inner complex crossed-lamellar/homogeneous layer.

The composite prismatic layer consists of radially aligned primary units made up of smaller crystallites radiating from a central axis (Plate 7, figs 1–5). Each of these smaller crystallites may be several mm. in length and 40 μ in diameter, but the size varies greatly from species to species. Each of these crystallites is surrounded by a sheath of organic matrix. Closer examination shows that each of the larger crystallites

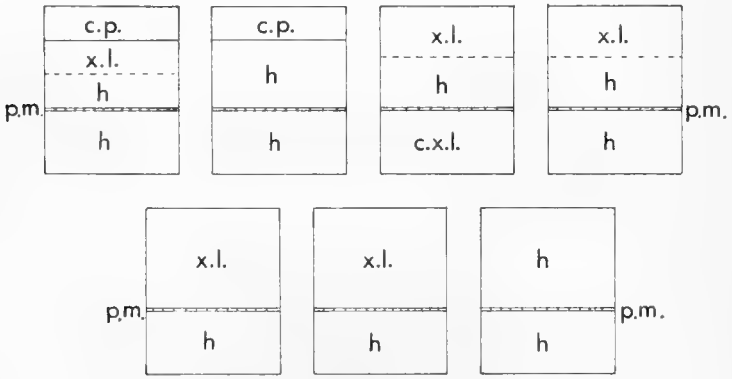


FIG. 17. Diagram showing the main types of shell layering found in the Veneracea. CP = composite prisms, CL = crossed-lamellar, CCL = complex crossed-lamellar, H = homogeneous, PM = pallial myostracum.

TABLE 15

VENERACEA

Species	Locality	Mineralogy	Outer layer	Middle layer	Inner layer	Pallial myostracum
Venerinae:						
Venus alata (Reeve)	Italy	Aragonite	Composite prismatic	Crossed-lamellar becoming homogeneous inwards	Homogeneous	Thin, prismatic
Venus striatula (da Costa)	Italy	Aragonite	Composite prismatic	Crossed-lamellar thin, becoming homogeneous inwards	Homogeneous	Thin, prismatic
[illegible]			[illegible]			
Hysteroconcha dione (Linnaeus)	West Indies	Aragonite	Crossed-lamellar homogeneous inwards	—	Homogeneous	Prismatic
Hysteroconcha multispinosa (Sowerby)	Ecuador	Aragonite	Crossed-lamellar	—	Complex crossed-lamellar/homogeneous	
Lamelliconcha paytensis (d'Orbigny)	Ecuador	Aragonite	Crossed-lamellar	—	Complex crossed-lamellar	Thin, prismatic
Lioconcha asperrima (Sowerby)	Ecuador	Aragonite	Composite prismatic	Crossed-lamellar	Homogeneous/ complex crossed-lamellar	Thin, prismatic
Lioconcha castrensis (Linnaeus)	Queensland	Aragonite	Crossed-lamellar/ becoming homogeneous inwards	—	Complex crossed-lamellar	Thin, prismatic
Macrocallista squalida (Sowerby)		Aragonite	Crossed-lamellar, becoming homogeneous inwards	—	Homogeneous	
Pitar affinis (Gmelin)	Indian Ocean	Aragonite	Crossed-lamellar	—	Homogeneous	Thin, prismatic
Pitar sp.	Ecuador	Aragonite	Crossed-lamellar	—	Homogeneous	Thin, prismatic

TABLE 15

VENERACEA

Species	Locality	Mineralogy	Outer Layer	Middle Layer	Inner Layer	Pallial Myostracum
Venerinae						
Venus alata (Reeve)	Italy	Aragonite	Composite prismatic	Crossed lamellar becoming homogeneous inwards	Homogeneous	Thin, prismatic
Venus striatula (da Costa)	Italy	Aragonite	Composite prismatic	Crossed-lamellar thin, becoming homogeneous inwards	Homogeneous	Thin, prismatic
Venus subimbricata Sowerby	Central America	Aragonite	Crossed lamellar, becoming homogeneous inwards		Homogeneous	Thin, prismatic
Venus verrucosa Linnaeus	Naples & Britain	Aragonite	Composite prismatic	Crossed lamellar, becoming homogeneous inwards	Homogeneous	Thin, prismatic
Circomphalus plicata (Gmelin)	West Africa	Aragonite	Finely crossed-lamellar becoming homogeneous inwards		Homogeneous	Indistinct
Periglypta reticulata (Linnaeus)	Torres Str.	Aragonite	Composite prismatic	Crossed lamellar, becoming homogeneous inwards	Complex crossed-lamellar with lenses of myostracal prisms	Prismatic
Circinae						
Circe crocea Gray	Red Sea	Aragonite	Crossed lamellar homogeneous inwards		Homogeneous	Indistinct
Circe intermedia (Reeve)	Aden	Aragonite	Crossed lamellar homogeneous inwards		Homogeneous	Thin, prismatic
Circe scripta (Linnaeus)	Indo-Pacific	Aragonite	Crossed lamellar homogeneous inwards		Complex crossed lamellar, prism sheets	Prismatic
Gafrarium divaricatum (Gmelin)	East Indies	Aragonite	Crossed lamellar homogeneous inwards		Complex crossed lamellar with myostracal prisms	Prismatic
Gafrarium pectinatum (Linnaeus)	Indian Ocean	Aragonite	Crossed lamellar homogeneous inwards		Complex crossed lamellar with myostracal prisms	Prismatic
Gafrarium tumidum Bolten	Seychelles	Aragonite	Crossed lamellar homogeneous inwards		Complex crossed-lamellar with myostracal prisms	Prismatic
Gouldia australis Angas	Australia	Aragonite	Finely crossed-lamellar		Homogeneous	
Gouldia cerina Gray	Bermuda	Aragonite	Finely crossed-lamellar		Homogeneous	
Sunetinae:						
Sunetta solandri (Gray)	Indian Ocean	Aragonite	Irregular crossed-lamellar passing into homogeneous inwards		Homogeneous	Prismatic
Meretricinae:						
Meretrix dillwyni Reeve	Indian Ocean	Aragonite	Finely crossed-lamellar homogeneous inwards		Homogeneous	Prismatic
Tivela hians (Phillips)	Ecuador	Aragonite	Composite prismatic	Homogeneous	Homogeneous	Prismatic, indistinct
Tivela ponderosa Koch	Aden	Aragonite	Crossed lamellar homogeneous inwards		Homogeneous	
Pitarinae:						
Agriopoma catharia Dall	Ecuador	Aragonite	Finely crossed-lamellar becoming homogeneous inwards		Homogeneous/ complex crossed-lamellar	Indistinct, prismatic
Amiantis erycina (Linnaeus)	Indian Ocean	Aragonite	Finely crossed-lamellar homogeneous inwards		Homogeneous	
Hysteroconcha dione (Linnaeus)	West Indies	Aragonite	Crossed lamellar homogeneous inwards		Homogeneous	Thin, prismatic
Hysteroconcha multisp[illegible] (Sowerby)	Ecuador	Aragonite	Crossed lamellar		Complex crossed lamellar, prism sheets	
Lamelliconcha paytensis (d'Orbigny)	Ecuador	Aragonite	Crossed lamellar		Complex crossed-lamellar	Thin, prismatic
Lioconcha asperrima (Sowerby)	Ecuador	Aragonite	Composite prismatic	Crossed-lamellar	Homogeneous, crossed-lamellar	Thin, prismatic
Lioconcha castrensis (Linnaeus)	Queensland	Aragonite	Crossed lamellar becoming homogeneous inwards		Complex crossed-lamellar	Thin, prismatic
Macrocallista spadicea (Sowerby)		Aragonite	Crossed lamellar, becoming homogeneous inwards		Homogeneous	
Pitar japonus (Gmelin)	Indian Ocean	Aragonite	Crossed lamellar		Homogeneous	Thin, prismatic
Pitar sp.	Ecuador	Aragonite	Crossed lamellar		Homogeneous	Thin, prismatic

TABLE 15 *Continued*

Species	Locality	Mineralogy	Outer layer	Middle layer	Inner layer	Pallial myostracum
Dosiniinae:						
Dosinia sp.	S. Carolina	Aragonite	Composite prisms	Crossed-lamellar becoming homogeneous inwards	Complex crossed-lamellar	Thin, prismatic
Dosinia annae Carpenter	Ecuador	Aragonite	Composite prismatic	Crossed-lamellar, homogeneous inwards	Complex crossed-lamellar	Thin, prismatic
Dosinia ponderosa (Gray)	Ecuador	Aragonite	Composite prismatic	Crossed-lamellar, homogeneous inwards	Complex crossed-lamellar	Thin, prismatic
Mercenaria mercenaria (Linnaeus)	England	Aragonite	Composite prismatic	Crossed-lamellar, becoming homogeneous inwards	Homogeneous	Thin, prismatic
Petricolidae:						
Petricola denticulata Sowerby	Ecuador	Aragonite	Crossed-lamellar	—	Complex crossed-lamellar	Thin, prismatic
Petricola pholadiformis Lamarck	Britain	Aragonite	Crossed-lamellar	—	Complex crossed-lamellar	Thin, prismatic
Petricola lithophaga (Retzius)	Mediterranean	Aragonite	Crossed-lamellar	—	Complex crossed-lamellar	
Cooperellidae:						
Cooperella subdiaphana Carpenter	California	Aragonite	Homogeneous	—	Homogeneous	
Species	Locality	Mineralogy	Outer layer	Middle layer	Inner layer	Pallial myostracum

TABLE 15 *Continued*

Species	Locality	Mineralogy	Outer layer	Middle layer	Inner layer	Radial myostracum
Desminae						
Desmia sp.	S. Carolina	Aragonite	Composite prisms	Crossed lamellar becoming homogeneous inwards	Complex crossed lamellar	Thin, prismatic
Desmia annae Carpenter	Ecuador	Aragonite	Composite prismatic	Crossed lamellar homogeneous inwards	Complex crossed-lamellar	Thin, prismatic
Desmia peltoides (Gray)	Ecuador	Aragonite	Composite prismatic	Crossed lamellar, homogeneous inwards	Complex crossed-lamellar	Thin, prismatic
Cyclinnae						
Cyclina chinensis (Bolten)		Aragonite	Crossed lamellar radial on outside, concentric inwards		Complex crossed lamellar	Thin, prismatic
Gemminae						
Gemma gemma (Totten)	U.S.A.	Aragonite	Crossed lamellar, becoming homogeneous inwards		Homogeneous	
Tapetinae						
Paphia textilis (Linnaeus)	China	Aragonite	Fine crossed lamella		Complex crossed-lamellar	Prismatic
Tapes litterata (Linnaeus)	Indian Ocean	Aragonite	Composite prismatic		Homogeneous	Thin, prismatic
Venerupis crenata (Lamarck)	Port Jackson	Aragonite	Composite prismatic	Crossed lamellar becoming homogeneous inwards	Homogeneous	Thin, prismatic
Chioninae						
Anomalocardia braziliana (Gmelin)	Brazil	Aragonite	Composite prismatic	Crossed lamellar, becoming homogeneous inwards	Homogeneous	Thin, prismatic
Chione stutchburyi (Gray)	New Zealand	Aragonite	Crossed lamellar homogeneous inwards		Complex crossed lamellar homogeneous	Prismatic
Chione gravida (Gmelin)	West Indies	Aragonite	Composite prismatic	Crossed lamellar, becoming homogeneous	Homogeneous	Thin, prismatic
Chione paphia (Linnaeus)	West Indies	Aragonite	Composite prismatic	Crossed lamellar becoming homogeneous inwards	Homogeneous	Prismatic
Chione undatella Sowerby	California	Aragonite	Crossed lamellar becoming homogeneous inwards		Homogeneous	Thin, prismatic
Chione subrugosa Sowerby	Ecuador	Aragonite	Composite prismatic	Crossed lamellar becoming homogeneous inwards	Homogeneous	Thin, prismatic
Chionopsis gnida (Sowerby & Broderip)	Ecuador	Aragonite	Composite prismatic	Crossed lamellar becoming homogeneous inwards	Homogeneous	Thin, prismatic
Lirophora effosa (Bivona)	Madeira	Aragonite	Crossed lamellar becoming homogeneous inwards		Homogeneous	Thin, prismatic
Lirophora peruviana (Sowerby)	Peru	Aragonite	Crossed lamellar, becoming homogeneous inwards		Homogeneous complex crossed lamellar	Thin, prismatic
Perothaca jedoensis (Lischke)	Japan	Aragonite	Composite prismatic	Crossed lamellar, homogeneous inwards	Homogeneous	Thin, prismatic
Mercenaria mercenaria (Linnaeus)	[illegible]	Aragonite	Composite prismatic	Crossed lamellar becoming homogeneous inwards	Homogeneous	Thin, prismatic
Petricolidae						
Petricola carditoides Sowerby	[illegible]	Aragonite	Crossed lamellar		Complex crossed-lamellar	Thin, prismatic
Petricola pholadiformis Lamarck	[illegible]	Aragonite	Crossed lamellar		Complex crossed-lamellar	Thin, prismatic
Petricola typica (Reeve)	[illegible]	Aragonite	[illegible]		[illegible]	
Cooperellidae						
Cooperella atlantica Carpenter	Carolina	Aragonite	Homogeneous		Homogeneous	
Species	Locality	Mineralogy	[illegible]	[illegible]	[illegible]	[illegible]

is made up of further smaller units about 0·5 μ in diameter and diverging in a feathery manner from the central axis of the larger crystallites (Plate 7, fig. 4).

The outer layer is separated by various degrees of distinctiveness from the underlying crossed-lamellar layer which has concentrically aligned primary lamels (Plate 7, fig. 1). This middle layer changes to homogeneous structure when traced towards the shell interior. In some species the distinctly crossed-lamellar portion of the layer is almost entirely suppressed (Plate 7, fig. 2). The crossed-lamellar and homogeneous portions of the shell cannot be designated as separate layers for they vary in extent both between and within a species.

In two layered Veneracea the outer part of the outer layer consists of crossed-lamellar structure (Plate 8, figs 2 & 4) which passes transitionally inwards into homogeneous structure (Plate 8, fig. 3). The orientation of the lamels in the outer layer is controlled by the type of shell margin present in each species. In the Veneracea the marginal areas are variable with margins which are reflected, inflected, shelf-like or combinations of these. A further complication to the shape of the shape of the margin may be ribbing and strong concentric sculpture. With a reflected shell margin the first order lamels in the outer region of the outer shell layer lie

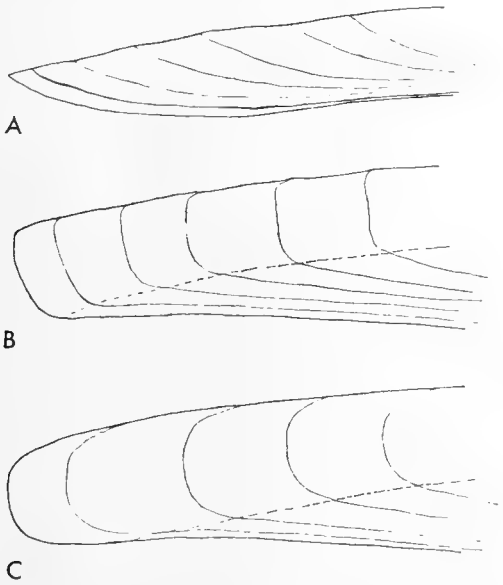


FIG. 18. Diagram showing radial sections of three types of shell margin found in the Veneracea. A. Here the margin is slightly reflected; there will be a gradual change from crossed-lamellar structure on the outside to homogeneous structure inwards. B. In this case the margin is strongly reflected and in the position marked by the dotted line there will be a sharp structural change. C. The margin is even more strongly reflected than in B and similarly there will be a sharp change in structure along the dotted line.

subparallel to the outer shell surface, although at the time of secretion, they were aligned normal to the secreting surface. With an inflected shell margin (Text-fig. 18) the first order lamels retain more of a concentric alignment. Again, when traced towards the shell interior the crossed-lamellae pass into homogeneous structure. The point at which the change takes place is usually where the reflection or inflection of growth lines changes rapidly. Further inwards from these points the growth increment lines are much more closely bunched suggesting a slower growth rate. The change from crossed-lamellar structure to homogeneous can thus be interpreted as a result of differential growth rates imposed by geometrical constraints caused by the shape of the shell margin.

In all cases the inner shell layer consists of complex crossed-lamellar or homogeneous structures or combinations of the two. Sheets of myostracal prisms are also common.

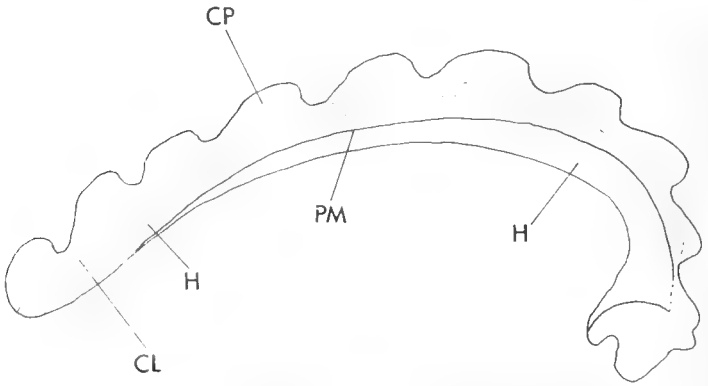


FIG. 19. Radial section of *Chione subrugosa*. CP = composite prismatic, CL = crossed-lamellar, h = homogeneous, PM = pallial myostracum.

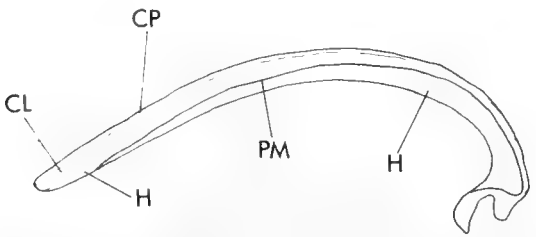


FIG. 20. Radial section of *Chamalea striatula*. CP = composite prisms, CL = crossed-lamellar, H = homogeneous, PM = pallial myostracum.

Subfamily **VENERINAE**

Most species in this group possess the three layered shell; composite prisms, crossed-lamellar/homogeneous and with one exception an inner homogeneous layer. Two species have only two layered shells. In *Periglypta puerpera* the inner layer is largely constructed of myostracal prisms with small areas of complex crossed-lamellar structure.

Subfamily **CIRCINAE**

All species in this group have the basic two layered shell. In most species there is a well defined prismatic pallial myostracum. The inner layer is variable; in the species of *Gafrarium* examined it is largely made up of myostracal prisms with small amounts of complex crossed-lamellar structure. In most other species it is homogeneous.

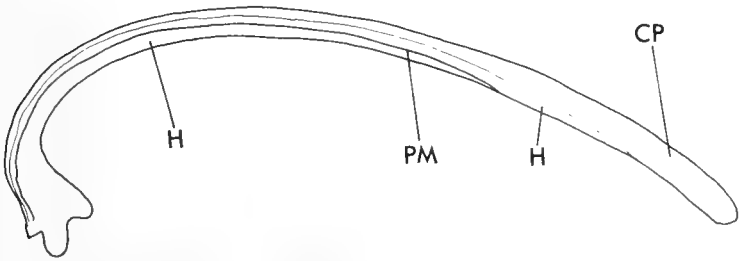


FIG. 21. Radial section of *Tivela hians*. CP = composite prisms, H = homogeneous, PM = pallial myostracum.

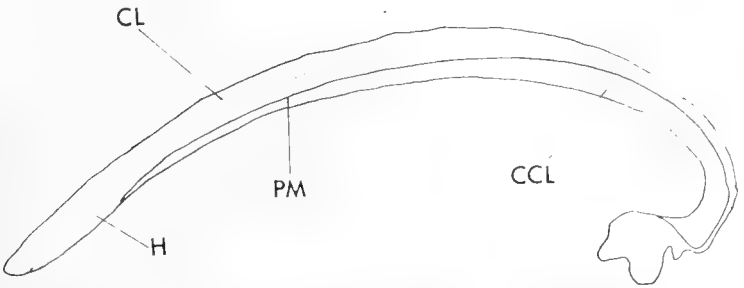


FIG. 22. Radial section of *Lioconcha castrensis*. CL = crossed-lamellar, H = homogeneous, PM = pallial myostracum, CCL = complex crossed-lamellar.

Subfamily **SUNNETINAE**

In *Sunetta solanderi* the margin is strongly reflected and the structure consists of outer crossed-lamellar structure, with the lamels radially aligned, which pass inwards into homogeneous structure. The inner layer is homogeneous with thin sheets of myostracal prisms.

Subfamily **MERETRICINAE**

In *Tivela hians* there is a three layered shell with the middle layer consisting entirely of homogeneous structure and also a homogeneous inner layer. *Tivela ponderosa* and *Meretrix* have a two layered shell.

Subfamily **PITARINAE**

Most of this family have a two layered shell but in *Lioconcha asperrima* there is an outer composite prismatic layer.

Subfamily **DOSININAE**

The three species examined in this group, all have a three layered shell, with an outer composite prismatic, a middle crossed-lamellar/homogeneous and an inner complex crossed-lamellar layer. A similar three layered shell has been described from *Dosinia japonica* by Kobayashi (1966).

Subfamily **CYCLININAE**

The one species examined has a two layered shell.

Subfamily **GEMMINAE**

Both species examined have a two layered shell.

Subfamily **TAPETINAE**

In *Tapes litterata* and *Venerupis* there is a three layered shell but only two layers in *Paphia textilis*.

Subfamily **CHIONINAE**

Both three and two layered shells are found in this family and the variation may be found within species of one genus. In *Mercenaria mercenaria* the crossed-lamellar portion of the middle layer is often indistinct but the structure is revealed by electron microscopy. Most species have an inner homogeneous layer.

Subfamily **PETRICOLIDAE**

This group has two layered shells; in the outer layer the crossed-lamellar structure does not grade inwards into homogeneous structure, as in most other Veneracea.

Subfamily **COOPERELLIDAE**

In the one species examined both layers consisted of homogeneous structure.

Order MYOIDA

MYACEA

(Plate 11, fig. 4; Text-figs 23–25)

Six species have been examined structurally and twelve mineralogically. The shell is aragonitic. The superfamily divides naturally into two groups the Corbulidae and the Myidae, these are discussed in turn.

In the family Corbulidae the shell is inaequivalve, the left valve being the smaller. The outermost part of the left valve consists solely of periostracum which fits like a flap against the right valve when the shell is closed (Yonge, 1946). In both valves, the periostracum may line the inner margin of the shell for some distance in preserved specimens. Two main shell layers are present, an outer crossed-lamellar layer which forms most of the hinge and an inner complex crossed-lamellar layer which is bounded by the trace of the pallial line. In the outer layer the lamels are arranged concentrically to the shell margin. In adult specimens where the growth rate is slower, marginal thickening has taken place and the periostracal flaps and extensions are frequently incorporated into the shell proper, by subsequent deposition. The periostracal flap of the left valve may even become incorporated into the shell of the right valve.

In most species there is a well developed pallial myostracum and within this there is the inner shell layer of complex crossed-lamellar structure which is fairly coarse. In all species there are commonly sheets of myostracal prisms interbedded with the normal structure. In *Corbula crassa* and *C. tunicata* there are well developed myostracal pillars arising from the trace of the pallial line.

In addition to the marginal periostracal flaps the animal appears capable of laying periostracum-like material down as a sheet, over all the inner surface of the shell. In some species, this happens several times in the life of the animal (Text-fig. 25).

In the family Myidae a rather different arrangement is seen, there being three distinct shell layers. There is an outer homogeneous layer, a middle crossed-lamellar layer and within the pallial line an inner layer which consists of either complex crossed-lamellar or homogeneous structures. The outer layer consists of granular crystals (Plate 11, fig. 4) about 5 μ in length and 2·5 μ in diameter with no obvious crystal form but with a slight elongation towards the shell margin. Although this layer is called homogeneous it differs from all other homogeneous

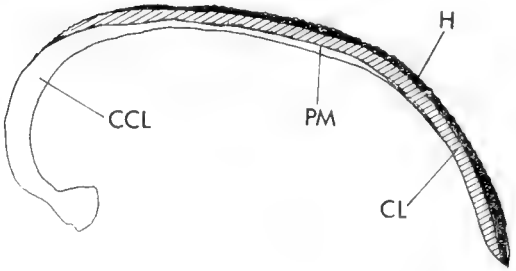


FIG. 23. Radial section of *Platydon cancellata*. H = homogeneous, CL = crossed-lamellar, PM = pallial myostracum, CCL = complex crossed-lamellar.

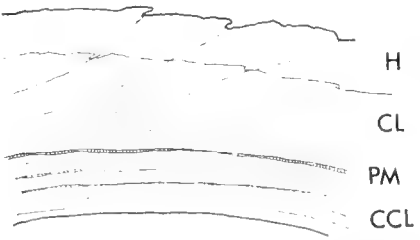


FIG. 24. Detail of shell layers in radial section of *Platydon cancellata*. H homogeneous, CL = crossed-lamellar, PM = pallial myostracum, CCL = complex crossed-lamellar.

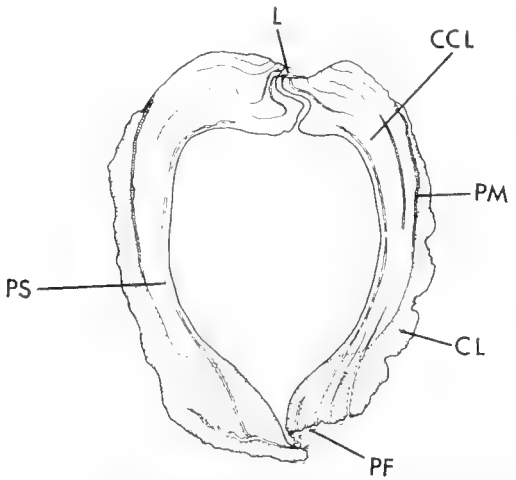


FIG. 25. Radial section of both valves of *Corbula gibba* showing the periostracal flaps (PF) and sheets (PS) incorporated into the shell a characteristic of this family. Other lettering; CL = crossed-lamellar, CCL = complex crossed-lamellar, PM = pallial myostracum, L = ligament.

structures we have recognized by appearing grey instead of brown in thin section. It is probable that the outer layer may have been derived by the degeneration of a phylogenetically earlier prismatic layer. The middle layer consists of very fine primary lamels, arranged concentrically. There is a thin, prismatic pallial myostracum in *Platydon cancellata* but only a sharp change in shell banding in *Mya arenaria*. Distinct sheets of myostracal prisms are often found in the inner layer.

GASTROCHAENACEA

Three species of this small superfamily of rock borers have been examined structurally and mineralogically. The shell is aragonitic.

The shell consists of two layers, an outer crossed-lamellar layer and an inner layer which may be complex crossed-lamellar or homogeneous. In all three species the outer layer has concentrically arranged lamels which pass transitionally inwards into homogeneous structure. The inner layer of *Gastrochaena gigantea* is complex crossed-lamellar but that of *G. ovata* and *G. truncata* is homogeneous, the former being distinctly lamellate. A thin prismatic pallial myostracum is present in all three species.

HIATELLACEA

(Plate 9, figs 1–4; Text-fig. 26)

This is a very small superfamily consisting of four extant genera, one of which *Panopea*, is divided into two subgenera *Panopea* and *Panomya*. Five species have been examined structurally and mineralogically, all are aragonitic.

In *Panopea* s.s. the shell consists of three layers, an outer simple prismatic layer which may be very thin, a middle homogeneous layer and an inner layer which may be homogeneous or complex crossed-lamellar. The simple prisms of the outer layer have rather irregular boundaries and orientations (Plate 9, fig. 1). They vary in width between 30–50 μ and are made up of smaller platy crystallites between 0·5–1·5 μ in width, which radiate from the central prism axis (Plate 9, fig. 3). The rate

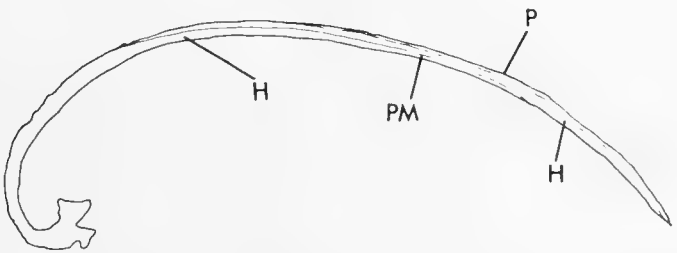


FIG. 26. Radial section of *Panopea zeylandica*. P = prisms, H = homogeneous, PM = pallial myostracum.

Table 16

MYACEA

Species	Locality	Mineralogy	Outer layer	Middle layer	Inner layer	Myostraca	
						Pallial	Adductor
Mya arenaria Linnaeus	Britain	Aragonite	Grey, granular homogeneous	Crossed-lamellar, fine	Finely complex crossed-lamellar with myostracal sheets	Prismatic	
Mya truncata Linnaeus	Britain	Aragonite	Grey, granular, homogeneous	Crossed-lamellar	Finely complex crossed-lamellar with myostracal sheets	Prismatic	
Platydon cancellata Conrad	California	Aragonite	Grey, granular, homogeneous	Crossed-lamellar	Complex crossed-lamellar with myostracal sheets	Prismatic, thin	
Corbula crassa Hinds	Japan	Aragonite	Crossed-lamellar	—	Complex crossed-lamellar with myostracal bands and pillars	Prismatic	Prismatic
Corbula gibba (Olivi)	Naples	Aragonite	Crossed-lamellar	—	Complex crossed-lamellar	Prismatic	
Corbula hydropica Iredale	Queensland	Aragonite	Crossed-lamellar	—	Complex crossed-lamellar with myostracal sheets and pillars	Prismatic	Prismatic
Caryocorbula amethystina Olsson	Ecuador	Aragonite	Crossed-lamellar	—	Complex crossed-lamellar with myostracal sheets and pillars	Prismatic	Prismatic

of divergence from the axis is high, so that the crystallites appear almost horizontal in relation to the axis (Plate 9, fig. 2). The middle homogeneous layer at high magnifications is seen to consist of short crystallites aligned in two directions (Plate 9, fig. 4) suggesting perhaps a transition to crossed-lamellar structure. The outer shell surface of *Panopea* is ornamented by granules arranged into rows radiating from the umbo.

In *Hiatella*, *Cyrtodaria* and *Panomya* there are only two layers. In all cases, the outer layer is homogeneous and excepting *Panomya* the inner layer is also homogeneous. In *Panomya* the inner layer may be homogeneous with thin prismatic sheets or it may consist of complex crossed-lamellar structure. In a specimen of *Hiatella arctica* from Spitzbergen the inner layer consisted almost entirely of myostracal prism sheets. Prismatic adductor myostraca were seen in *Panomya norvegica* and *Hiatella arctica*.

The presence of the outer simple prismatic layer in *Panopea* may be of considerable phylogenetic significance and this is discussed further in the conclusions.

PHOLADACEA

(Plate 10, figs 1–4; Plate 11, figs 1–3; Text-figs 27–29)

Two families constitute this superfamily the Pholadidae and the Teredinidae; these are discussed separately.

Eleven species of Pholadidae have been examined structurally and mineralogically; all species examined consisted of aragonite. Two main types of shell structure were found in this family. In three species examined there was a three layered shell consisting of an outer simple prismatic layer, a middle crossed-lamellar layer and an inner complex crossed-lamellar or homogeneous layer. The outer layer consists of prisms (Plate 11, fig. 3) very similar to those found in *Panopea* (Hiatellacea p. 34);

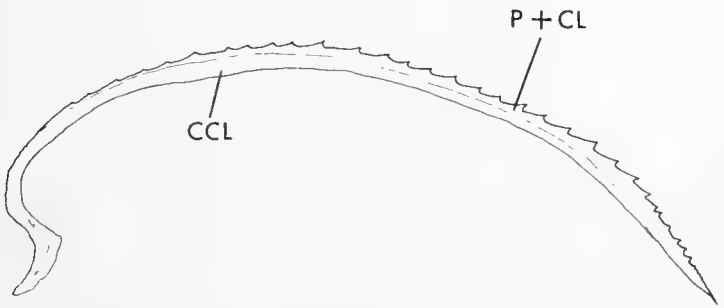


Fig. 27. Radial section of *Barnea candida*, as shown in Text-fig. 28 there is an interdigitation of the outer prismatic layer with the middle crossed-lamellar layer making differentiation at this magnification difficult. P = prisms, CL = crossed-lamellar, CCL = complex crossed-lamellar.

TABLE 17

GASTROCHAENACEA

Species	Locality	Mineralogy	Outer layer	Inner layer	Pallial myostracum
Gastrochaena gigantea Deshayes	India	Aragonite	Crossed-lamellar/homogeneous	Complex crossed-lamellar	Prismatic, thin
Gastrochaena ovata Sowerby	Panama	Aragonite	Crossed-lamellar/homogeneous	Complex crossed-lamellar	Prismatic, thin
Gastrochaena truncata Sowerby	Mazatlan	Aragonite	Crossed-lamellar/homogeneous	Homogeneous	Prismatic, thin

TABLE 18

HIATELLACEA

Species	Locality	Mineralogy	Outer layer	Middle layer	Inner layer	Pallial myostracum
Panopea zeylandica (Quoy & Gaimard)	New Zealand	Argonite	Simple prisms	Homogeneous	Homogeneous or complex crossed-lamellar	Prismatic
Panopea australis Sowerby	Australia	Argonite	Simple prisms	Homogeneous	Homogeneous or complex crossed lamellar	Prismatic
Panopea (*Panomya*) *norwegica* (Spengler)	North Sea	Aragonite	Homogeneous		Complex crossed-lamellar or homogeneous with prism sheets	Prismatic
Cyrtodaria siliqua (Spengler)	British Columbia	Aragonite	Homogeneous		Homogeneous	Prismatic
Hiatella arctica (Linnaeus)	Britain	Aragonite	Homogeneous		Homogeneous	Prismatic

the prisms are irregular in size, length, and orientation in contrast to the more regular arrangement found, for example, in the Unionacea. The prismatic layer is not deposited continuously, for as seen in Text-fig. 28, the imbricating concentric ornament of this family is formed by a cyclical deposition and non-deposition of the prismatic structure (Plate 11, figs 1–2). A ventral 'shoot' of crossed-lamellar structure corresponds with each period of non-deposition of prisms. The crossed-lamellar layer is usually thin and the first order lamels short and coarse. The inner layer within the pallial line may be homogeneous or complex crossed-lamellar and is frequently lamellate and may contain sheets of myostracal prisms.

In *Zirfaea crispata* there is also a three layered shell but the outer layer consists of grey homogeneous structure. The individual crystallites (Plate 10, figs 1 & 2) are approximately 5–10 μ long and 2–4 μ wide with a slightly elongate shape. In this species the concentric ornament consists entirely of homogeneous structure. The structure resembles that of the Myidae and is conceivably derived from the simple prisms described above for other pholads.

In all other species of Pholadidae examined there is a two layered shell, with the outer ribbing and ornament being formed from crossed-lamellar structure. The

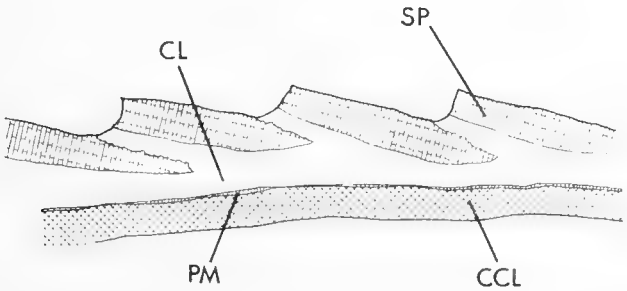


FIG. 28. Detail of radial section of *Barnea candida* showing the alternation of prismatic and crossed-lamellar structure in the outer layer. SP = simple aragonite prisms, CL = crossed-lamellar, PM = pallial myostracum, CCL = complex crossed-lamellar.

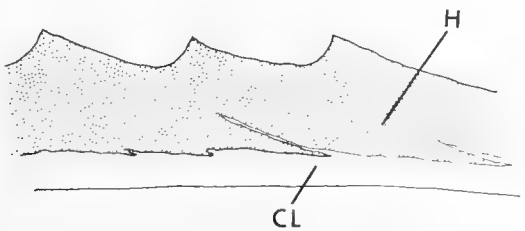


FIG. 29. Detail of a radial section of *Zirfaea crispata* showing outer homogeneous (H), and middle crossed-lamellar layer (CL).

strong umbonal reflections characteristic of the Pholadacea are formed from complex crossed-lamellar structure. Deposits of myostracal prisms occur beneath the adductor, pallial and other muscle attachment sites.

One species of Teredinae was examined structurally and mineralogically. The shell and tube are both aragonite.

The shell is nearly hemispherical in shape and complicated as in the Pholadidae by apophyses, shelves and condyles associated with the wood-boring habit (Turner, 1966). The shell is basically two layered, with an outer crossed-lamellar (Plate 10, figs 3 & 4) and an inner complex crossed-lamellar layer. The outermost part of the outer layer shows strongly reflected growth lines and the crossed-lamels are consequently radially aligned. In addition the lamels are very fine and present an almost homogeneous appearance. The complex crossed-lamellar layer is restricted to the umbonal ridge. Pads of myostracal prisms were seen beneath the large posterior adductor and beneath the anterior adductor which is situated on the umbonal reflection. The ventral condyle has homogeneous structure.

The calcareous tube which is secreted by the mantle surrounding the siphon tips consists of layers of irregular granular crystals about 5–10 μ in diameter.

Sub-Class *ANOMALODESMATA*

Order PHOLADOMYINA

PHOLADOMYACEA

(Plate 12, figs 1–4)

Because of lack of available material of this rare superfamily only a small fragment of *Pholadomya candida* was studied. It is aragonitic.

The shell is basically three layered with an outer very thin simple prismatic layer a middle nacreous layer and within the pallial line an inner nacreous inner (Plate 12, fig. 1). The thin outer layer (Plate 12, fig. 1) also forms the surface granules arranged in radiating rows from the umbo. The middle nacreous layer appears to be 'Treppen' structure of Wise (1970) (Plate 12, fig. 4) and the inner nacre to be sheet nacre. The inner part of the inner layer consists of alternations of thin sheets of nacre with layers of myostracal prisms which form the dominant component (Plate 12, figs 2 & 3). Because of the very limited sampling it is not certain how typical the myostracal prism layers are of the whole shell.

PANDORACEA

(Plate 13, figs 1–4; Text-figs 30 & 31)

Sixteen species were examined structurally and mineralogically. The shell is aragonitic throughout.

Representatives from all seven families recognized by Moore (1969) were examined and two distinct structural arrangements were found. One of these, with both layers consisting of homogeneous structure, is found in the Thracidae alone; all the

TABLE 19

PHOLADACEA

Species	Locality	Mineralogy	Outer layer	Middle layer	Inner layer	Myostraca	
						Pallial	Adductor
Barnea candida (Linnaeus)	Britain	Aragonite	Prismatic	Crossed-lamellar	Complex crossed-lamellar	Prismatic	
Pholas chiloensis Molina	Ecuador	Aragonite	Prismatic	Crossed-lamellar	Complex crossed-lamellar	Prismatic	
Pholas dactylus Linnaeus	Britain	Aragonite	Prismatic	Crossed-lamellar	Complex crossed-lamellar	Prismatic	
Parapholas acuminata (Sowerby)	Ecuador	Aragonite	Crossed-lamellar	—	Complex crossed-lamellar	Prismatic	

POROMYACEA

Species	Locality	Mineralogy	Outer layer	Middle layer	Inner layer	Pallial myostraca
Euciroa eburnea (Wood-Mason & Alcock)	Andamans	Aragonite	Simple prisms	Lenticular nacre	Sheet naclre	Prismatic, thin
Verticordia deshayesiana (Fischer)	Atlantic	Aragonite	Simple prisms	Lenticular nacre	Sheet nacre	Prismatic
Pecchiola argentea Savi & Meneghini	Italy	Aragonite	Simple prisms	Lenticular nacre	Sheet nacre	Prismatic
Poromya granulata (Nyst & Westendrop)	Britain	Aragonite	Homogeneous	Nacre	Sheet nacre	Prismatic
Cuspidaria arctica (Sars)	Norway	Aragonite	Homogeneous	—	Homogeneous	Indistinct
Cuspidaria chinensis (Griffith & Pidgeon)	Borneo	Aragonite	Homogeneous	—	Homogeneous	
Cuspidaria rostrata (Spengler)	Britain	Aragonite	Homogeneous	—	Homogeneous	Indistinct

TABLE 19

PHOLADACEA

Species	Locality	Mineralogy	Outer layer	Middle layer	Inner layer	Myostraca	
						Pallial	Adductor
Barnea candida (Linnaeus)	Britain	Aragonite	Prismatic	Crossed-lamellar	Complex crossed-lamellar	Prismatic	
Pholas chiloensis Molina	Ecuador	Aragonite	Prismatic	Crossed-lamellar	Complex crossed-lamellar	Prismatic	
Pholas dactylus Linnaeus	Britain	Aragonite	Prismatic	Crossed-lamellar	Complex crossed-lamellar	Prismatic	
Parapholas acuminata (Sowerby)	Ecuador	Aragonite	Crossed-lamellar		Complex crossed-lamellar	Prismatic	
Martesia striata (Linnaeus)	Trinidad	Aragonite	Crossed-lamellar		Complex crossed-lamellar	Prismatic	
Pholadidea loscombiana Turton	Britain	Aragonite	Crossed-lamellar		Complex crossed-lamellar	Prismatic	
Zirfaea crispata (Linnaeus)	Britain	Aragonite	Grey, granular, homogeneous	Crossed-lamellar	Complex crossed-lamellar	Prismatic	Prismatic
Teredo navalis (Linnaeus)	Britain	Aragonite	Crossed-lamellar		Complex crossed-lamellar	Prismatic	Prismatic

TABLE 20

PANDORACEA

Species	Locality	Mineralogy	Outer layer	Middle layer	Inner layer	Myostraca	
						Pallial	Adductor
Pandora arcuata Sowerby	Ecuador	Aragonite	Simple prisms	Lenticular nacre	Sheet nacre	Thin, prismatic	Prismatic
Pandora albida (Roding)	Naples	Aragonite	Simple prisms	Lenticular nacre	Sheet nacre		
Pandora trilineata Say	Eastern U.S.A.	Aragonite	Simple prisms	Lenticular nacre	Sheet nacre		
Periploma inaequale Schumacher	Jamaica	Aragonite	Simple prisms	Lenticular nacre	Sheet nacre	Thin, prismatic	
Offadesma angasi (Crosse & Fischer)	Australia	Aragonite	Simple prisms	Nacre	Sheet nacre		
Laternula anatina (Linnaeus)		Aragonite	Simple prisms	Lenticular nacre	Sheet nacre		
Myadora brevis Sowerby		Aragonite	Simple prisms	Lenticular nacre	Sheet nacre and myostracal prisms	Prismatic	Prismatic
Myadora striata (Quoy & Gaimard)	Auckland	Aragonite	Simple prisms	Lenticular nacre	Sheet nacre and myostracal prisms	Prismatic	
Myadora tasmanica Wood	Tasmania	Aragonite	Simple prisms	Lenticular nacre	Sheet nacre and myostracal prisms	Prismatic	
Cleidothaerus albidus Lamarck	N.S. Wales	Aragonite	Simple prisms	Lenticular nacre	Sheet nacre	Prismatic	Prismatic
Myochama anomioides (Stutchbury)	Australia	Aragonite	Simple prisms	Lenticular nacre	Sheet nacre	Prismatic	Prismatic
Kennerlya sp.	California	Aragonite	Simple prisms	Lenticular nacre	Sheet nacre	Prismatic	
Thracia convexa Wood	Britain	Aragonite	Homogeneous		Homogeneous	Trace	
Thracia phaseolina (Lamarck)	Britain	Aragonite	Homogeneous		Homogeneous	Trace	
Thracia villosiuscula (Macgillivray)	Britain	Aragonite	Homogeneous		Homogeneous		

TABLE 21

POROMYACEA

Species	Locality	Mineralogy	Outer layer	Middle layer	Inner layer	Pallial myostracum
Lucinoma chuna (Wood-Mason & Alcock)	Andamans	Aragonite	Simple prisms	Lenticular nacre	Sheet nacre	Prismatic, thin
Verticordia deshayesiana (Fischer)	Atlantic	Aragonite	Simple prisms	Lenticular nacre	Sheet nacre	Prismatic
Pecchiolia arcuata Savi & Meneghini	Italy	Aragonite	Simple prisms	Lenticular nacre	Sheet nacre	Prismatic
Poromya granulata (Nyst & Westendrop)	Britain	Aragonite	Homogeneous	Nacre	Sheet nacre	Prismatic
Cuspidaria arctica (Sars)	Norway	Aragonite	Homogeneous		Homogeneous	Indistinct
Cuspidaria chaceana (Griffith & Pidgeon)	Borneo	Aragonite	Homogeneous		Homogeneous	
Cuspidaria rostrata (Spengler)	Britain	Aragonite	Homogeneous	—	Homogeneous	Indistinct

other families have a three layered shell consisting of an outer simple prismatic layer a middle lenticular nacre layer and an inner sheet nacre layer. The outer simple prism layer is very thin and frequently worn off much of the shell. In most species examined a thin pallial myostracum separated the middle and inner nacreous layers. In *Myadora striata* most of the inner layer consists of myostracal prisms. Radial rows of granules are present on the outside of the shell in many species.

In the three species of *Thracia* examined, the two layered shell consists of homogeneous structure in both layers. Two species were examined at high magnifications and the inner surface of the shell appears granular with irregular crystals about 3 μ in diameter. In section these crystals are slightly flattened and have a slightly laminar arrangement. On the outside of the shell patterns of granules are seen (Tebble, 1966, fig. 103), when these are examined more closely they are seen to be isolated spherulitic structures (Plate 13, figs 1–4). These spherulites are made up of smaller crystallites (Plate 13, fig. 3) about 3 μ in length. The spherules form columnar growths intercalated with layers of periostracum (Plate 13, fig. 2). Eventually as growth proceeds these spherulites merge together and the crystal arrangement passes into a uniform homogeneous structure.

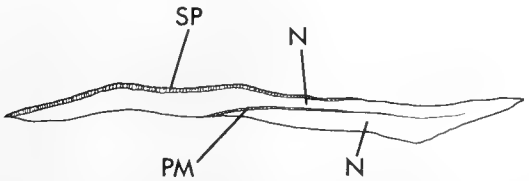


FIG. 30. Radial section of the flat right valve of *Pandora albida*. SP = aragonite simple prisms, N = nacre, PM = pallial myostracum.

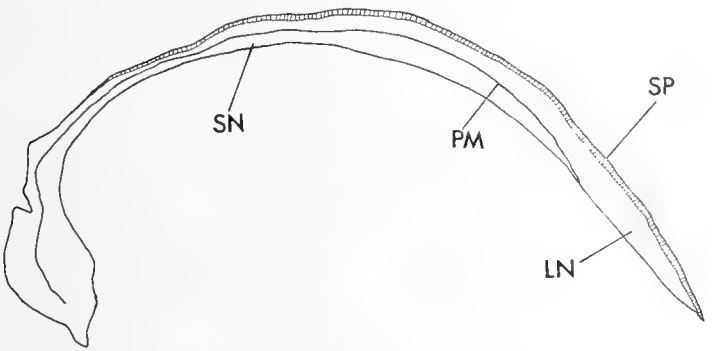


FIG. 31. Radial section of *Cleidothaerus albida*. SP = simple prisms, LN = lenticular nacre, PM = pallial myostracum, SN = sheet nacre.

Order POROMYOIDA

POROMYACEA

(Plate 13, figs 5; Plate 14, figs 1–5)

Seven species were examined structurally and mineralogically. The shell is aragonitic.

This superfamily is represented by three families, the Poromyidae, the Cuspidaridae and the Verticordidae. The latter have a three layered shell consisting of an outer, simple prismatic layer, a lenticular nacre a middle layer and a sheet nacre inner layer. The middle and inner layers are separated by a thin sheet of pallial myostracal prisms. The shell structure is generally similar to that of most of the Pandoracea; in *Euciroa* the prisms are irregular (Plate 13, fig. 5) and resemble those of *Panopea* (Hiatellacea). In *Poromya granulata* there is a three layered shell as above but the outer layer consists of granular homogeneous structure probably phylogenetically derived from a structural breakdown of simple prismatic structure (Plate 14, figs 2 & 4).

The Cuspidaridae and some Poromyidae both have a two layered shell with homogeneous structure in both layers. The granules of the homogeneous layers are about 2 μ in size (Plate 14, fig. 5) and generally similar in appearance to those of the Thracidae. The pallial myostracum was indistinct in the species examined and shows a discontinuity rather than a distinct structure.

CLAVAGELLACEA

(Plate 15, figs 1–5; Text-fig. 32)

This is a small highly aberrant superfamily which consists of three extant genera *Clavagella, Humphreysia* and *Penicillus* which show a progressive fusion of the true shell with the calcareous tube. The valves are however free when young. Three species were examined structurally and mineralogically; the shell and tube are both aragonite.

In *Clavagella aperta* the valves are fairly large and only one is fused with the siphonal tube. The valves consist of a thin simple prismatic outer layer with a sheet nacre inner layer. Thin sheets of myostracal prisms are secreted beneath the muscle attachment scars.

Valves of a juvenile *Humphreysia strangei* were examined, these had a simple prismatic outer layer and inner sheet nacre layers (s). The outside of the valves is finely pustulate.

In *Penicillus* s.s. the true shell is seen as two valves occupying a saddle shaped area incorporated into the side of the tube (Text-fig. 32). The tube is extended posteriorly as a hollow cylinder and anteriorly as a perforated disc (the watering pot). The true valves are covered by a thin periostracum which is inserted from the outside of the shell to line the inside of the tube at the edge of the saddle shaped area. The valves consist of two layers, an outer extremely thin simple prismatic layer with an

TABLE 22

Superfamily	Mineralogy	Aragonite simple prisms	Calcite simple prisms	Composite prisms	Lenticular nacre	Sheet nacre	Foliated	Crossed-lamellar	Complex crossed-lamellar	Homogeneous	Myostracal pillars	Tubules
Nuculacea	A	·	·	X	X	X	·	·	·	X	·	·
Nuculanacea	A	·	·	·	·	·	·	·	·	·	·	·

TABLE 22

SUPERFAMILY	MINERALOGY	ARAGONITE SIMPLE PRISMS	CALCITE SIMPLE PRISMS	COMPOSITE PRISMS	LENTICULAR NACRE	SHELLY NACRE	FOLIATED	CROSSED LAMELLAR	COMPLEX CROSSED LAMELLAR	HOMOGENEOUS	MYOSTRACAL PILLARS	HIPPURITES
Nuculacea	A	.		X	X	X					.	
Nuculanacea	A	.	.	.	.					X	.	
Solemyacea	A	X	.	.	.				.	X	.	
Arcacea	A	.		.	.			X	X		X	X
Limopsacea	A	.		.	.		.	X	X	.	X	X
Mytilacea	A + C	.	X	.	X	X					.	X
Pinnacea	A + C	.	X	.	X	X			.		.	
Pteriacea	A + C	.	X	.	X	X			X		.	
Pectinacea	A + C	.	X	.	.	.	X	X	X		.	X
Anomiacea	A + C	.	.	.	.	.	X	X			.	.
Limacea	A + C	.		.	.		X	X		.	.	.
Ostreacea	A + C	.	X	.	.		X				.	
Unionacea	A	X	.	.	X	X	.	.	.		.	
Trigonacea	A	X	.	.	X	X	.	.	.		.	
Lucinacea	A	.	.	X	.		.	X	X		X	X
Chamacea	A*	.	.	.	.	.		X	X		X	X
Leptonacea	A	.	.	.	.			X	X	X	.	
Chlamydoconchacea	.	.		.	.	.					.	.
Cyamiacea	A	.		.	.				.	X	.	
Carditacea	A	.		.	.			X	X		X	X
Crassatellacea	A	.		.	.	.		X	X	X	X	X
Cardiacea	A	.		.	.			X	X	.	.	.
Tridacnacea	A	.		.	.		.	X	X		.	
Mactracea	A	.		.	.			X	X		.	
Solenacea	A	.		.	.			X	X	X	.	
Tellinacea	A	.	.	X	.	.		X	X	X	.	
Dreissenacea	A	.	.	.	.	.	.	X	X	.	.	
Gaimardiacea	A	.	.	.	.	.	.	.		X	.	.
Arcticacea	A	.		.	.		.	X	X	X	.	
Glossacea	A	.	.	.	.	.	.	X	X	X	.	
Corbiculacea	A	.	.	.	.	.	.	X	X	.	.	occ
Veneracea	A	.	.	X	.	.	.	X	X	X	.	
Myacea	A	X?	.		.	.	.	X	X	X	.	.
Gastrochaenacea	A	.	.	.	.	.	.	X	X	X	.	.
Hiatellacea	A	X	.	.	.	.		.	X	X	.	.
Pholadacea	A	X			.	.	.	X	X	X	.	
Pholadomyacea	A	X	.	.	X	X	.	.	.	.		.
Pandoracea	A	X	.	.	X	X	.	.	.	X	.	.
Poromyacea	A	X	.	.	X	X	.		.	X	.	.
Clavagellacea	A	X	.	.	.	X	.	.		.	.	.

inner sheet nacreous layer about 500 μ thick (Plate 15, figs 1 & 2). The outer shell surface is ornamented with small granules radiating from the umbo (Plate 15, fig. 5). The outer more irregular part of the saddle shaped area consists of homogeneous structure and is lain down on the inside of the nacreous layer. On the inner surface of the homogeneous layer, is the attachment of the pallial muscles which secrete beneath them, myostracal prisms forming a conspicuous 'W' shaped scar. The tube and pot form the most conspicuous part of the animal. Optically the shell structure of these features appears homogeneous with conspicuous lamellate banding. Electronmicroscopy shows that both the tube and pot are made up of platy crystals 0·5–2 μ in diameter, 0·3–0·5 μ in width irregular in outline but aligned with the long axis parallel with the outside of the tube. (Plate 15, figs 2 & 4).

The mode of secretion of the pot and tube pose problems; both of these two structures lie external to the periostracum which is not in intimate contact with the tube but encases the long siphons (Purchon, 1956). On many specimens growth increments can be seen at the posterior end of the tube and this must be formed by

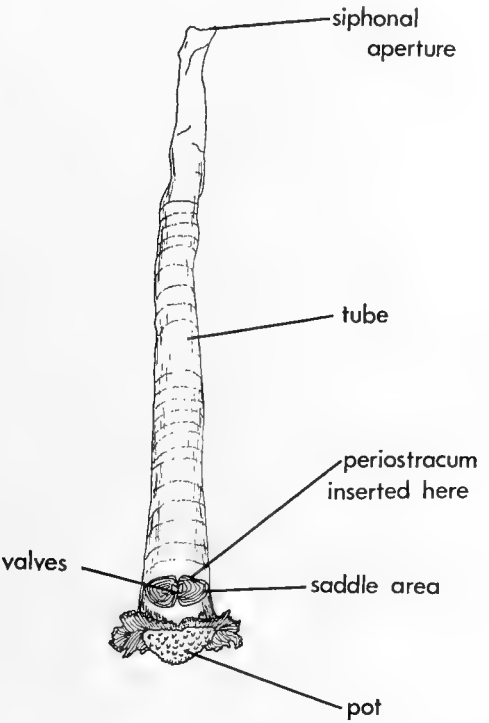


FIG. 32. Sketch showing the main features of the shell of *Penicillus* sp.

mantle at the tips of the siphons. However it is difficult to see how the pot could be formed as a continuous growth process without repeated resorbtion. It is possible that the tube and pot are secreted only when the animal is near fully grown. The common occurrence of sand, pebbles, shells and other debris incorporated into the pot and tube, together with the general lack of growth lines, is slight evidence in favour of a rapid secretion process. The posterior end of the tube, grows subsequently by the addition of material by the tips of the siphons; in this case we see clear growth increments and no debris incorporated into the shell. However, until more is known about the biology of *Penicillus*, we have no real evidence to support either alternative explanation of shell secretion.

CONCLUSIONS

It has become increasingly clear that the Bivalvia cannot be classified on single character systems (Cox, 1960; Newell, 1965) and that a total organism study involving shell characters, comparative anatomy, geological history and more recently biochemical characters must be employed or attempted (Ghiselin *et al*, 1967). Shell microstructure and mineralogy can therefore be only contributory evidence towards establishing the relationships of the bivalves and must be used in conjunction with other characters. However, our shell structure studies have established twelve characters which can be used as an aid to classification; in some cases these characters can be crucial evidence (Kennedy, Morris & Taylor, 1970).

The classifications of Newell (1956, 1969) and Cox (1960) are essentially similar and are compilations of existing knowledge from the single and multiorgan systems of previous neontologists, geological history and the relationships of fossil forms established on shell characters alone. This is in contrast to the single organ classifications of for example Purchon (1959), Atkins (1938). If the shell structure combinations we have recognized are superimposed upon these compilations of previous knowledge, it is possible to see where these characters support or are in apparent disagreement with the established classification. A summary of shell characters arranged in the classificatory order of Newell (1969, Treatise of Invertebrate Palaeontology) is shown in Table 22. There is a striking general agreement of shell structure characters with classification.

The relationship of the bivalve superfamilies and their shell structures is best seen in the form of a phylogenetic tree[1], showing the geological history possible ancestry and known shell structure combinations (Text-fig. 33).

It is apparent that many bivalve superfamilies or lineages have long and continuous records extending far back into the Palaeozoic and in many cases have been extremely conservative. Major evolutionary radiations are seen in the early Ordovician, Permo-Trias and of the heterodonts in the Mesozoic; the latter is discussed by Stanley (1967). Shell structure information at critical points of radiation in the Palaeozoic is almost non-existent. This information would be extremely

[1] The construction of this tree has been carried out in close collaboration with Dr. N. J. Morris and draws heavily upon his wide knowledge of Palaeozoic and Mesozoic bivalves.

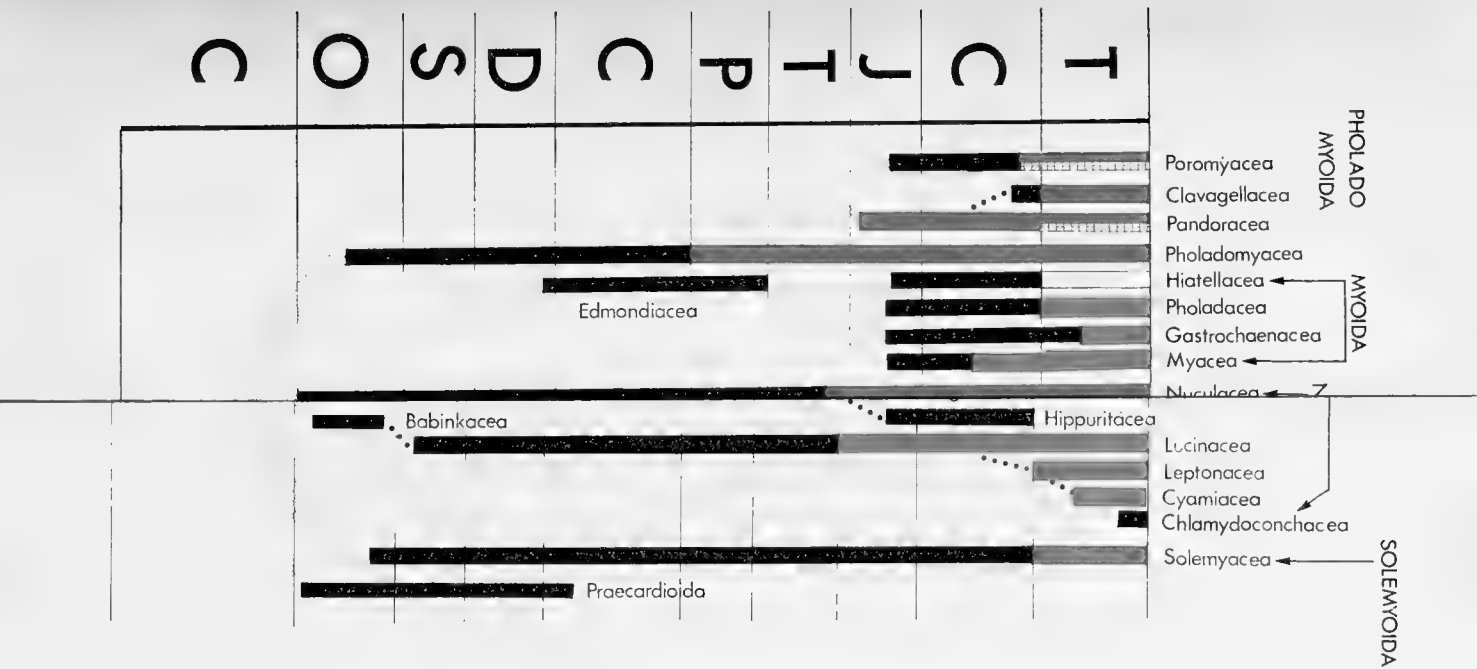


FIG. 33. Geological history and possible phylogeny of the Bivalvia. The main shell structure groupings (colours) have been superimposed on the superfamily lineages.

Orange	= Crossed-lamellar/complex crossed-lamellar	Yellow	= Composite prisms/crossed-lamellar, complex crossed-lamellar.
Blue (continuous)	= Aragonite simple prisms/nacre.	Blue (broken)	= Calcite prisms/nacre.
Green	= Foliated structure.	Brick pattern	= Homogeneous.
Black	= Unknown.	Stippled	= Areas of uncertain relationships.

The Hiatellacea are mainly homogeneous but *Panopea* has an outer simple aragonite prismatic layer. This layer is also present in some Pholadacea which have middle crossed-lamellar and inner complex crossed-lamellar layers. Calcite prism outer layers are found in the Ostreacea and some Pectinacea.

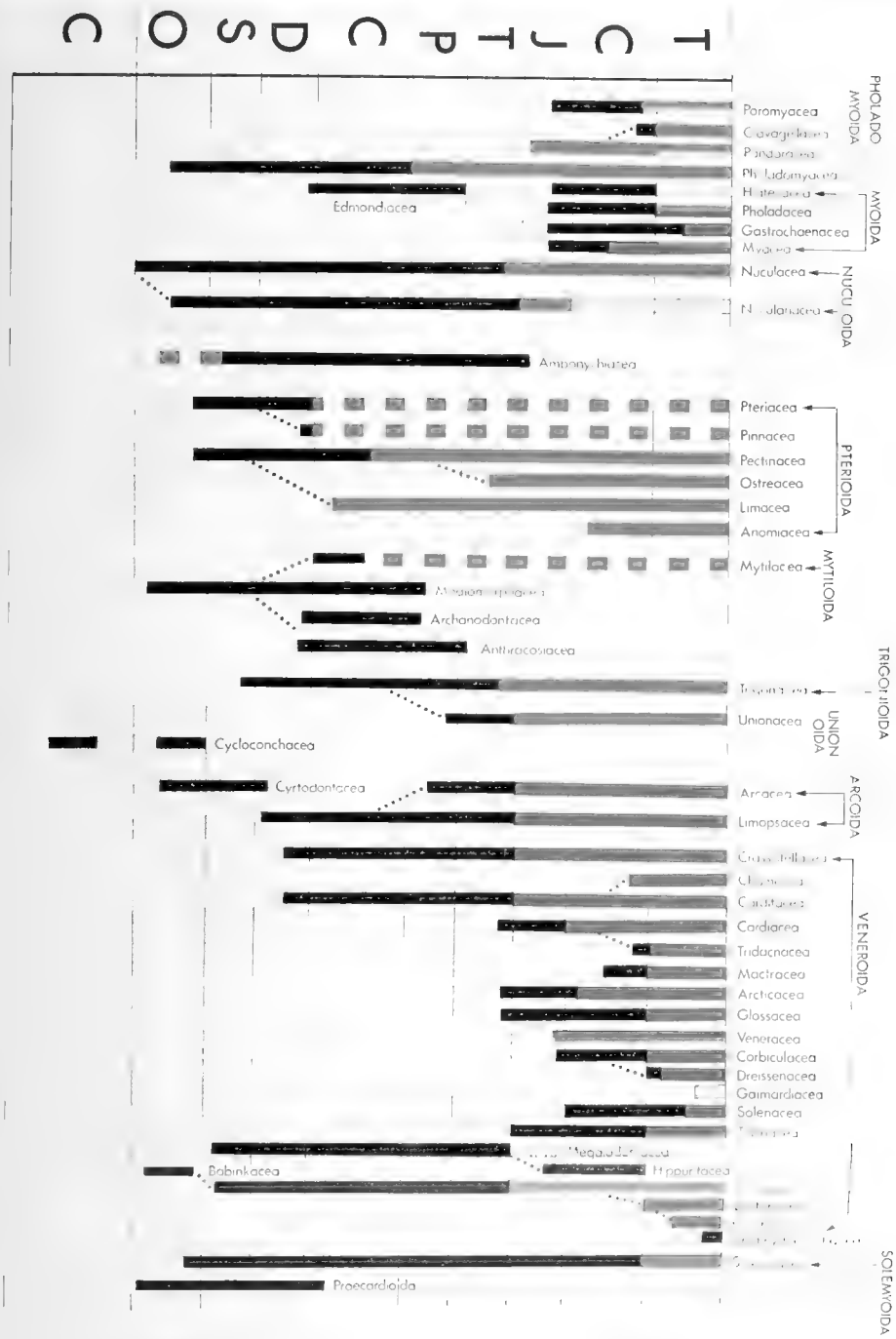


FIG. 33. Geological history and possible phylogeny of the Bivalvia. The main shell structure [illegible] imposed on the superfamily [illegible]

Orange	[illegible]	[illegible]	[illegible]
Blue (continuous)	= Aragonite simple prisms na	[illegible]	[illegible]
Green	[illegible]	[illegible]	[illegible]
Black	= Unknown	[illegible]	[illegible]

The Hiatellacea are mainly homogeneous but [illegible] some Pholadacea which have middle crossed lam[illegible] the Ostreacea and some Pectinacea

important in the Ordovician where most of the radiation of the major lineages and shell structure combinations probably took place. However because of dissolution, recrystallisation and replacement the original shell fabrics have disappeared or have been altered out of recognition.

The relationships of the various bivalve superfamilies are discussed in terms of shell structure variations below.

Subclass *PALAEOTAXODONTA*

Two superfamilies belong in this group; the Nuculacea are generally regarded as the most primitive living bivalves (Yonge, 1959) but the other superfamily the Nuculanacea are considered to be as highly specialized as any similar group throughout the bivalves (Yonge, 1959). The origin of the Nuculacea can be traced back to the Upper Cambrian *Ctenodonta* (Cox, 1959) and the group appears to have remained relatively unchanged morphologically throughout their subsequent history. The nacreous and composite prismatic shell is different from that of any other family. However, we consider that the difference between simple aragonite prisms (possibly the ancestral condition) such as found in the Unionacea and Pholadomyacea and the composite prisms of the Nuculacea is slight and arises from differences in the degree of mantle reflection at the shell margin. The extant Nuculanacea have a homogeneous shell but as shown by Cox (1959) and Taylor, Kennedy & Hall (1969) this has not always been the case.

Subclass *CRYPTODONTA*

Solemya has been considered to be a protobranch (Palaeotaxodonta) by Yonge (1939, 1959) but as Newell (1965) has pointed out, it is becoming increasingly apparent that the Solemyacea have been separated from the rest of the protobranchs from at least the Devonian and are not obviously related to the Nuculacea. The shell structure and in particular the character of the outer prismatic layer, is distinctive, but nevertheless can be readily derived from simple aragonite prisms. Our observations tend to support Newell's opinion that the Solemyacea belong to a separate subclass the Cryptodonta.

The extinct Palaeozoic order Praecardioida is placed in the Cryptodonta, but there is very little evidence of any relationship to the Solemyacea. We have no shell structure information on this group.

Allen & Sanders (1969) have recently described the anatomy and discussed the affinities of the Recent genus (*Nucinella* classified in the Limopsacea, in the Treatise) which they consider to be a monomyarian 'solemyid' and possibly related to the extinct actinodont group (i.e. Cycloconchacea). Although there are several anatomical resemblances of *Nucinella* to *Solemya* other characters resemble those of the Nuculacea. Our observations of the shell structure show that it is homogeneous structure similar to that of *Nuculana* but unlike *Solemya* or the Nuculacea. But if *Nucinella* is either a nuculacean or a solemyacean then reference to Text-fig. 33 will show that both these groups were probably derived from a cycloconchacean ancestor.

Subclass *PTERIOMORPHIA*

The Arcacea are generally thought to be derived from the Cyrtodontacea of the lower Ordovician (Cox, 1959, 1960) but as pointed out by Morris (1967) the connection is not firmly established. Newell (1954) has considered that the 'cyrtodontids' are also the ancestors of the Pteriacea, Pectinacea and also possibly the Mytilacea. These latter groups probably became separate from the "cyrtodontid stock" rather earlier (Text-fig. 33). The Arcacea have a crossed-lamellar and complex crossed-lamellar shell structure with tubules and myostracal pillars. This structure is very different from that of the rest of the Pteriomorphia, but similar to that of some heterodonts such as the Carditacea. The only character which is common between the Arcacea and the rest of the Pteriomorphia is the filibranch gill and it seems to us that there is no close relationship between the groups and the Arcoida (Arcacea & Limopsacea) should possibly be considered as a separate subclass related to the Heterodonta. This does not of course deny a once common ancestry.

The Mytilacea have a very distinctive prismatic, calcitic, outer shell layer, sometimes called 'fibrillar' (Oberling, 1964). This particular structure is found in no other bivalve group. The work of Osborn (1970) on mammalian teeth has shown that all the different prism-like structures may not be very different from each other. The Mytilacea may have arisen directly from the lower Ordovician-Permian family the Modiomorphidae and have no apparent derivatives. Newell (1965) placed the Pinnacea in the order Mytiloida (implying relationship) but the simple calcite prisms, general shell form and anatomy suggest derivation from the Pteriacea.

As mentioned above the Pteriacea and the Pectinacea are both considered to have been derived from a cyrtodontid ancestor (Cox, 1960; Newell, 1938). Although they have different shell structures this does not rule out a common ancestor. The occurrence of an outer prismatic layer in oysters, the early post larval stages of some pectens (Jackson, 1890) and in some species of *Propeamussium* suggests that the foliated layer in these forms may have originally been derived from aragonite nacreous structure by a change in the calcium carbonate polymorph. The superfamily Ambonychiiacea which ranges from middle Ordovician to upper Devonian has been extensively discussed by Pojeta (1966); it includes many *'Pteria'*-like forms. Recently we have examined an *Ambonychia* from the upper Ordovician (Ashgill) from near Girvan, Scotland which has some shell structure preserved. As might be expected it showed nacreous inner layers, but unfortunately the outer layer was recrystallised, but was probably calcite prisms.

Newell & Boyd (1970) have recently described the earliest known members of the Anomiacea, from the Permian. This superfamily is probably derived from the Pectinacea. The same is probably true of the Limacea. The Ostreacea first appeared in the Permian and were probably derived from a Pectinacean ancestor the Pseudomonotidae (Newell, 1961; Newell & Boyd, 1970). The shell structure characters support this suggestion.

Subclass *PALAEOHETERODONTA*

The Unionacea and Trigonacea have a very similar shell structure of aragonite simple prisms and lenticular and sheet nacreous layers. There has long been debate as to the possible relationship of these two families (Cox, 1960). The anatomical evidence suggests that they may be distinct groups, whereas the palaeontological evidence is ambiguous and unsatisfactory. As well as the morphological and shell structure similarities, they have a character in common which is usually overlooked; this is the possession of calcareous gill spicules recorded for the Unionacea by Ridewood (1904) and for the Unionacea and Trigonacea (Atkins, 1938). They are the only bivalve superfamilies to possess these spicules.

Subclass *HETERODONTA*

The Lucinacea are known from the Silurian to Recent and can be traced through the Babinkacea back to the middle Ordovician (McAlester, 1965, 1966). McAlester has argued that the Lucinacea are a distinct bivalve group and should be considered as a separate subclass. Certainly the Lucinacea have been distinct for a long period of time and only the Leptonacea and Cyamiacea can be related to them. However Boss (1969) considers from anatomical and shell morphological evidence that the Lucinacea are closely connected to other bivalves of the heterodont subclass. The Lucinacea have a three layered shell of an outer composite prismatic layer, a middle crossed-lamellar layer and an inner complex crossed-lamellar layer. This combination is also found in the Tellinacea and some Veneracea. The shell structure evidence thus supports the opinion of Boss (1969) that the Lucinacea belong to the Heterodonta, but reference to Text-figure 33 will show that they have been distinct from the rest of the heterodont stock for a long time.

The Tellinacea are known from the Upper Triassic to Recent but their phylogenetic relationships are obscure. As noted above the three layered shell structure is found in the Lucinacea and Veneracea. The Solenacea may have arisen from the Tellinacea in the late Cretaceous or early Cainozoic (Davies, 1935; Morris, 1967). In the process they must have lost the outer composite prismatic layer, as indeed have some of the Tellinacea.

The Astartacea, Carditacea, Chamacea, Cardiacea, Tridacnacea, Mactracea, Arcticacea, Veneracea, Corbiculacea, Dreissenacea and the Glossacea all appear to be generally related (Text-fig. 33). The shell structure is generally similar in all these groups with only relatively small variations (Table 22). The most important variation is the three layered shell in some Veneracea. Most of these families arose in the Mesozoic and Cainozoic, and Stanley (1968) has discussed this spectacular radiation. The most striking trend is the appearance and extensive radiation of the infaunal siphonate feeders, which Stanley relates to the development of siphons and the closure of the mantle cavity by mantle fusion. Most of the families involved in this radiation have a two layered shell of crossed-lamellar structure and complex crossed-lamellar structures. In some families one or both layers may consist of homogeneous structure, but in these cases it is obviously derived from the structures mentioned.

The Mesozoic Veneroida were probably derived from either the Crassatellacea (Stanley, 1968), which first appeared in the Devonian, or from the Carditacea which also appeared in the Devonian (Morris, 1967). These two families probably have a common origin in the lower Palaeozoic from a cyrtodontacean stock (Text-fig. 33). Yonge, (1969) has recently stressed the similarities between the Crassatellacea and the Carditacea.

The Chamacea which first appeared in the upper Cretaceous are thought on the basis of shell structure and anatomical characters to have been derived from the Carditacea (Kennedy, Morris & Taylor, 1970).

The Cardiacea first appeared in the Trias, but no obvious ancestor can be cited from older rocks. The Tridacnacea can be readily derived from the Cardiacea in the Eocene or late Cretaceous (Stasek, 1962). The Mactracea appear similar to the Cardiacea in shell structure details but there is no real evidence of any relationship.

The Arcticacea, Veneracea and Corbiculacea may have been derived from the Jurassic forms *Pseudotrapezium* and *Pronella* (Casey, 1952; Morris, 1967). The Arcticacea and the Veneracea are probably very closely related. Although *Arctica* shows a homogeneous shell structure traces of crossed-lamellar structure may sometimes be seen. Other members of the Arcticacea show crossed-lamellar and complex crossed-lamellar structure. The Veneracea show two distinct types of shell structure; this may be a result of the loss of the outer composite layer in some forms or a polyphyletic origin for the Veneracea.

The Dreissenacea are a group of fresh water byssate anisomyarian bivalves which appeared in the Cainozoic. Because of their mytilid-like shell, their relations have remained obscure, but it has been realized for some time that they are unrelated to the Mytilacea (Yonge & Campbell, 1968). The shell structure shows great similarity in micro-details to that of the Corbiculacea and it is reasonable to suppose that the Dreissenacea arose from the fresh and brackish water Corbiculacea. Morton (1970) has made a study of the morphological changes seen in fossil forms, demonstrating a progression from the Corbiculacea to the Dreissenacea. However, the idea of some relationship to the Mytilacea has not entirely disappeared (Purchon & Brown, 1969).

Subclasses *MYOIDA* and *PHOLADOMYOIDA*

The Myoida and Pholadomyoida although classified in separate subclasses show obvious similarities and we consider that all the superfamilies in these subclasses can be derived from a "pholadomyacean" stock which has been in existence since the middle Ordovician. Other workers however, consider the resemblances to be the result of morphological convergence (Runnegar, 1966, 1967).

Pholadomya s.s. has a shell structure of simple aragonite prisms and middle and inner nacreous layers. *Panopea* of the Hiatellacea (Myoida) is anatomically and morphologically very similar to *Pholadomya* (even including surface granules) but has an outer prismatic layer, a middle homogeneous and an inner complex crossed-lamellar later. Other members of the Hiatellacea have shells consisting of homogeneous structure alone. It seems very probable that the Hiatellacea have been

derived from the "pholadomyoid" stock. Some Pholadacea have a shell structure of simple prisms, crossed-lamellar and complex crossed-lamellar layers. The structure of the outer layer closely resembles that of *Panopea*. It seems that the Pholadacea may have arisen from the Pholadomyacea in the early Jurassic; the genera *Myopholas* and *Giradotia* would seem to be transitional forms (Morris, unpub.).

The Myacea consist of two families, the Myidae (Palaeocene-Recent) and the Corbulidae (L. Jurassic-Recent). It does not seem very likely on anatomical and shell morphological grounds that the Corbulidae gave rise to the Myidae. This is supported by the fact that the Corbulidae have a two layered and the Myidae a three layered shell. The origin of the Corbulidae might perhaps be found in the Permian pholadomyoid forms such as *Pyramus* amd *Megadesmus* (see figures in Runnegar, 1967). The Myidae would seem to have been independently derived from the "pholadomyoid" stock at a much later date.

Most Pandoracea have a shell structure of simple prisms and two nacreous layers, this and anatomical characters suggest a derivation from the Pholadomyacea in the Trias or lower Jurassic. The Thracidae (family of Pandoracea) have today a largely homogeneous shell, the outermost part of which retains a vestige of prismatic structure. However in the Cretaceous the Thracidae had a prismato-nacreous shell and apart from shell structure there is little to differentiate the Thracidae, from other Pandoracean families such as the Laternulidae.

The origins of the Poromyacea are obscure but certainly the Cuspidariidae can be traced back to the Trias (Cox, 1960; Morris, 1967) and have probably arisen from the Edmondiacean genus *Solenomorpha*. The Edmondiacea appear to be a heterogeneous Palaeozoic group closely related to the Pholadomyacea. Some of the Poromyacea have a prismato-nacreous shell and others are entirely homogeneous. Although the superfamily has a septibranch gill there are many anatomical resemblances to the Pandoracea.

The Clavagellacea are a highly aberrant group but anatomical characters, the nacreo-prismatic shell and the surface granules suggest a close affinity with the Pandoracea.

Evidence from the Monoplacophora (Erben, *et al*, 1968), Archaeogastropoda (Wise, 1970; Wise & Hay, 1968), *Nautilus* (Grégoire, 1962) and some of the oldest bivalve lineages strongly suggests that the "primitive" shell structure of the bivalves is a simple aragonite prism outer layer and middle and inner nacreous layers. Subsequent evolutionary radiation of the shell structures has been a result of the increased exploitation of different habitats and different modes of life. Taylor & Layman (1972) have stressed the functional significance of bivalve shell structures and present evidence correlating structure with mode of life. However we need much more information on the course of evolutionary change in shell structures and it is probable that in time sufficient well preserved Palaeozoic material will be discovered in order to document these changes.

ACKNOWLEDGEMENTS

We are very grateful for the constant interest, assistance and advice of Dr. Noel Morris, particularly in the preparation of the conclusions.

We should also like to thank Dr. R. P. S. Jefferies, Mr. R. J. Cleevely and Mr. C. P. Palmer for advice and assistance in various ways. We are especially grateful to the staff of the electron microscope unit at the British Museum (Natural History) under the direction of Mr. B. Martin for patient advice and assistance.

REFERENCES

Allen, J. A., & Sanders, H. L. 1969. *Nucinella serrei* Lamy (Bivalvia: Protobranchia) a monomyarian solemyid and possible living actinodont. *Malacologia*, **7** : 381–396.

Atkins, D. 1937. On the ciliary mechanisms and interrelationships of Lamellibranchs. Part III: Types of Lamellibranch gill and their food currents. *Q. Jl. microsc. Sci.*, **79** : 375–421.

—— 1938. On the ciliary mechanisms and interrelationships of lamellibranchs. VII, Latero-frontal cilia of the gill filaments and their phylogenetic value. *Q. Jl. microsc. Sci.*, **80** : 346–436.

Boggild, O. B. 1930. The shell structure of the mollusks. *K. danske Vidensk. Selsk. Skr.*, **2** : 232–325.

Boss, K. J. 1968. New species of Vesicomyidae from the Gulf of Darien, Caribbean Sea (Bivalvia, Mollusca). *Bull. mar. Sci.*, **18** : 731–748.

—— 1969. Lucinacea and their heterodont affinities (Bivalvia). *Nautilus*, **82** : 128–131.

Boyd, D. W., & Newell, N. D. 1968. Hinge grades in the evolution of crassatellacean bivalves as revealed by Permian genera. *Am. Mus. Novit.*, **2328** : 52.

Casey, R. 1952. Some genera and subgenera, mainly new, of Mesozoic heterodont lamellibranchs. *Proc. malac. Soc. Lond.*, **29** : 121–176.

Cox, L. R. 1959. The geological history of the Protobranchia and the dual origin of taxodont Lamellibranchia. *Proc. malac. Soc. Lond.*, **33** : 200–209.

—— 1960. Thoughts on the classification of the Bivalvia. *Proc. malac. Soc. Lond.*, **34** 60–88.

Davies, A. M. 1935. *Tertiary Faunas*. Vol. 1. *The composition of Tertiary faunas*. 406 pp. London.

Erben, H. K., Flajs, G., & Siehl, A. 1968. Über die Schalenstruktur von Monoplacophoren. *Akad. Wiss. Lit. Mainz.* 1968, no. 1 : 1–24.

Ghiselin, M. T., Degens, E. T., Spencer, D. W., & Parker, R. H. 1967. A phylogenetic survey of molluscan shell matrix proteins. *Breviora*, **262** : 1–35.

Grégoire, C. 1962. On the submicroscopic structure of the *Nautilus* shell. *Bull. Inst. r. Sci. nat. Belg.*, **38** : 1–71.

Hamilton, G. H. 1969. The taxonomic significance and theoretical origin of surface patterns on a newly discovered bivalve shell layer, the mosaic-ostracum. *Veliger*, **11** : 185–194.

Jackson, R. T. 1890. Phylogeny of the Pelecypoda, the Aviculidae and their allies. *Mem. Boston Soc. nat. Hist.*, **4** : 277–400.

Kennedy, W. J., Morris, N. J., & Taylor, J. D. 1970. The shell structure, mineralogy, and relationships of the Chamacea (Bivalvia). *Palaeontology*, **13** : 379–413.

Kobayashi, I. 1966. Submicroscopic observations on the shell structure of Bivalvia—Part II. *Dosinia* (*Phacosoma*) *japonica* Reeve. *Sci. Rep. Tokyo Kyoiku Daig., Sect. C*, **9** : 189–210.

Lowenstam, H. A. 1954. Factors affecting the aragonite : calcite ratios in carbonate secreting marine organisms. *J. Geol.*, **62** : 284–322.

LOWERSTAM, H. A. 1964. Coexisting calcites and aragonites from skeletal carbonates of marine organisms and their strontium and magnesium contents. *In: Recent Researches in the fields of Hydrosphere, Atmosphere and Nuclear Geochemistry*, 373–404, Tokyo.

MCALESTER, A. L. 1965. Systematics, affinities, and life habits of *Babinka*, a transitional Ordovician lucinoid bivalve. *Palaeontology*, **8** : 231–246.

—— 1966. Evolutionary and systematic implications of a transitional Ordovician lucinoid bivalve. *Malacologia*, **3** : 433–439.

MOORE, R. C. (EDITOR). 1969. *Treatise on Invertebrate Palaeontology* (*Part N*), *Mollusca* 6 (*Bivalvia*). 2 vols., 950 pp., Univ. of Kansas, Geological Soc. of America.

MORRIS, N. J. 1967. Scaphopoda and Bivalvia. Chapter 17 in: *The Fossil Record. A symposium with documentation.* Geol. Soc. London, pp. 469–77.

MORTON, B. 1970. The evolution of the heteromyarian condition in the Dreissenacea (Bivalvia). *Palaeontology*, **13** : 563–572.

NEWELL, N. D. "1937" 1938. Late Palaeozoic pelecypods: Pectinacea. *Bull. Kans. Univ. geol. Surv.*, **10** (1) : 1–123.

—— 1942. Late Palaeozoic pelecypods: Mytilacea. *Bull. Kans. Univ. geol. Surv.*, **10** (11) : 1–80.

—— 1954. Status of invertebrate palaeontology, 1953, V. Mollusca. *Bull. comp. Zool. Harv.* **112** : 161–172.

—— 1960. The origin of the oysters. *Internatl. Geol. Congr., Rept. 21st Sess., Norden* **2** : 81–86.

—— 1965. Classification of the Bivalvia. *Am. Mus. Novit.*, **2206** : 1–25.

—— & BOYD, D. W. 1970. Oyster-like Permian Bivalvia. *Bull. Am. Mus. nat. Hist.* **143** : 1–281.

OBERLING, J. J. 1964. Observations on some structural features of the Pelecypod shell. *Mitt. naturf. Ges. Bern*, **20** : 1–63.

—— & BOSS, K. J. 1970. Observations on the shell structure of *Calyptogena* (Vesicomyidae; Bivalvia; Mollusca). *Revue Suisse Zool.*, **77** : 91–90.

OSBORN, J. W. 1970. The mechanism of prism formation in teeth: a hypothesis. *Calc. Tiss Res.*, **5** : 115–132.

POJETA, J. 1966. North American Ambonychiidae. *Palaeontogr. Am.*, **5** : 133–241.

PURCHON, R. D. 1956. A note on the biology of *Brechites penis* (L.) (Lamellibranchia). *J. Linn. Soc. Zool.*, **53** : 43–54.

PURCHON, R. D. 1959. Phylogenetic classification of the Lamellibranchia, with special reference to the Protobranchia. *Proc. malac. Soc. Lond.*, **33** : 224–230.

—— & BROWN, D. 1969. Phylogenetic interrelationships among families of bivalve molluscs. *Proc. Third Europ. Malac. Congr., Malacologia*, **9** : 163–171.

RIDEWOOD, W. G. 1903. On the structure of the gills of the Lamellibranchiata. *Phil. Trans R. Soc., ser. B*, **195** : 147–284.

RUNNEGAR, B. 1966. Systematics and biology of some desmodont bivalves from the Australian Permian. *J. geol. Soc. Aust.*, **13** : 373–386.

—— 1967. Desmodont bivalves from the Permian of Eastern Australia. *Bull. Bur. Miner. Resour. Geol. Geophys. Aust.*, **96** : 1–83.

STANLEY, S. M. 1967. Post-Palaeozoic adaptive radiation of infaunal bivalve molluscs—a consequence of mantle fusion and siphon formation. *J. Paleont.*, **42** : 214–229.

STASEK, C. R. 1962. The form, growth and evolution of the Tridacnidae (Giant Clams). *Archs. Zool. exp. gen.*, **101** : 1–40.

TAYLOR, J. D., & KENNEDY, W. J. 1969. The shell structure and mineralogy of *Chama pellucida* Broderip. *Veliger*, **11** : 391–398.

——, —— & HALL, A. 1969. The shell structure and mineralogy of the Bivalvia. Introduction, Nuculacea-Trigonacea. *Bull. Br. Mus. nat. Hist., Zool., Suppl.*, **3** : 1–125.

—— & LAYMAN, M. 1972. The mechanical properties of bivalve (Mollusca) shell structures. *Palaeontology*, **15** : 73–57..

TEBBLE, N. 1966. *British bivalve seashells.* British Museum (Natural History), 212 pp.
TRUEMAN, E. R. 1942. The structure and deposition of the shell of *Tellina tenuis*. *J. Roy. microsc. Soc.*, **62** : 69–92.
TURNER, R. D. 1966. A survey and illustrated catalogue of the Teredinidae. *Harv. Mus. Comp. Zool., Spec. Publ.*, 265 pp.
WISE, S. W. 1970. Microarchitecture and mode of formation of nacre (mother of pearl) in pelecypods, gastropods and cephalopods. *Eclog. geol. Helv.*, **63** : 775–797.
—— & HAY, W. W. 1968. Scanning electron microscopy of molluscan shell ultrastructures. II. Observations of growth surfaces. *Trans. Am. microsc. Soc.*, **87** : 419–430.
YONGE, C. M. 1939. The protobranchiate Mollusca: a functional interpretation of their structure and evolution. *Phil. Trans. Roy. Soc. ser. B*, **230** : 79–147.
—— 1946. On the habits and adaptations of *Aloidis* (*Corbula*) *gibba*. *J. Mar. Biol. Assoc. U.K.*, **26** : 358–376.
—— 1959. The status of the Protobranchia in the bivalve Mollusca. *Proc. malac. Soc. Lond.*, **33** : 210–214.
—— 1969. Functional morphology and evolution within the *Carditacea* (Bivalvia). *Proc. malac. Soc. Lond.*, **38** : 493–527.
—— & CAMPBELL, J. 1968. On the heteromyarian condition in the Bivalvia with special reference to *Dreissena polymorpha* and certain Mytilacea. *Trans. R. Soc. Edinb.*, **68** : 21–43

J. D. TAYLOR
Department of Zoology
BRITISH MUSEUM (NATURAL HISTORY)
CROMWELL ROAD
LONDON SW7 5BD

W. J. KENNEDY
Department of Geology and Mineralogy
UNIVERSITY OF OXFORD
PARKS ROAD
OXFORD

A. HALL
Department of Geology
UNIVERSITY OF LONDON
KING'S COLLEGE
STRAND
LONDON, WC2

PLATE 1

All figures on this plate are acetate peels

FIG. 1. Radial section of the outer composite prismatic layer of ***Codakia tigerina*** showing the fine needle-like crystallites aligned normal to the growth increments. ×160

FIG. 2. Radial section of ***Lucina fijiensis*** showing complex crossed-lamellar inner layer (bottom) with step-like blocks of pallial myostracum (upper). ×160

FIG. 3. Radial section of the outer crossed-lamellar layer of ***Astarte sulcata*** showing very fine first order lamels and growth increments. ×160

FIG. 4. Radial section of the outer layer of ***Astarte sulcata*** illustrating the change in orientation of the first order lamellae inwards from the outside of the shell (upper). ×100.

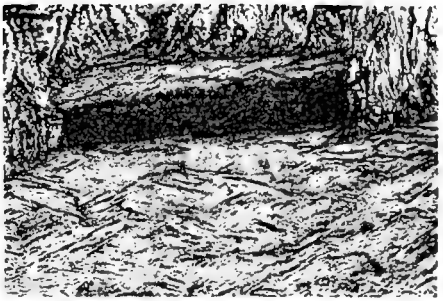
FIG. 5. Radial section of the inner complex crossed-lamellar layer of ***Lucina fijiensis.*** ×100.

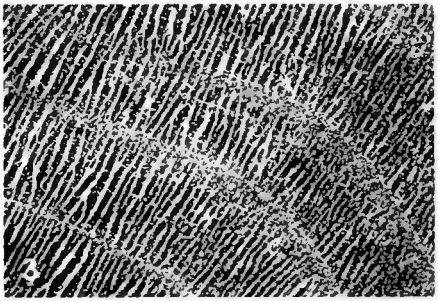
FIG. 6. Radial section of ***Crassatella decipiens*** showing the outer crossed-lamellar layer (top), the pallial myostracum and the inner layer which begins as complex crossed-lamellar but grades into homogeneous structure. ×160.

FIG. 7. Radial section of the inner layer of ***Astarte incrassata*** showing both the myostracal prisms and homogeneous structures. ×160.

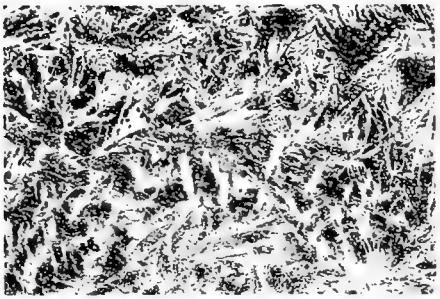
FIG. 8. Oblique section through the inner layer of ***Astarte incrassata*** in the umbonal area showing the individual myostracal prisms surrounded by homogeneous structure. ×80.

1




3

4



6

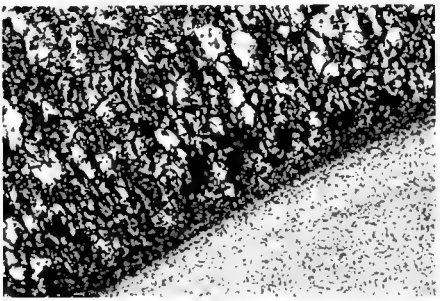


PLATE 2

FIG. 1. ***Crassatella radiata***, radial section showing myostracal pillars in the inner complex crossed-lamellar layer. These terminate at the inner shell surface to produce boss-like structures as in fig. 2. Acetate peel, × 160.

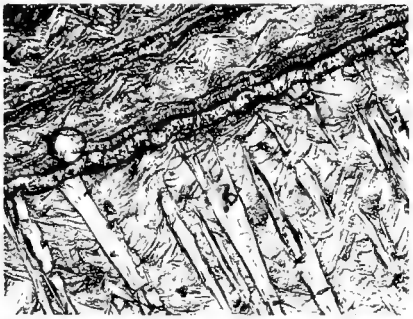
FIG. 2. Surface of the inner layer of ***Astarte borealis*** showing the high density of myostracal bosses, separated by homogeneous structure. Scanning electron-micrograph, × 50.

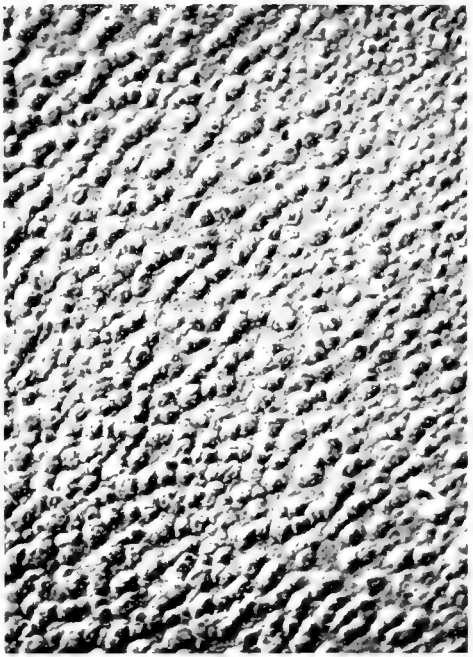
FIG. 3. Similar area to Fig. 2 but higher magnification. × 280.

FIG. 4. Radial section of the outer crossed-lamellar layer of ***Cardita sowerbyi*** showing how the primary lamels are arranged radially in the outer part of the shell (top) and become aligned concentrically inwards. Acetate peel, × 160.

FIG. 5. Radial section of ***Cardita marmorea*** showing the myostracal pillars cutting both the outer crossed-lamellar layer (bottom) and the inner complex crossed-lamellar layer. Acetate peel, × 160.

FIG. 6. Radial section of the inner complex crossed-lamellar layer of ***Cardita sowerbyi.*** Note the sheets of myostracal prisms and the continuity of the major structures through them. Acetate peel, × 160.





3

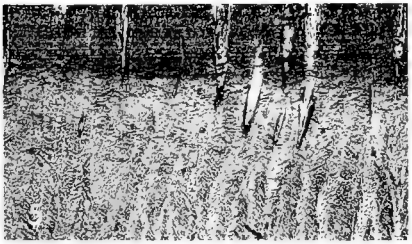


PLATE 3

FIG. 1. Radial section of ***Trachycardium consors*** in the hinge showing the crossed-lamellar layer with two orientations of first order lamels (top and bottom) separated by a thin myostracum (probably pedal). Acetate peel, × 160.

FIG. 2. Radial section of the outer crossed-lamellar layer of ***Acanthocardia echinata*** showing the very fine, first order lamels intersected by prominent growth banding. Acetate peel, × 160

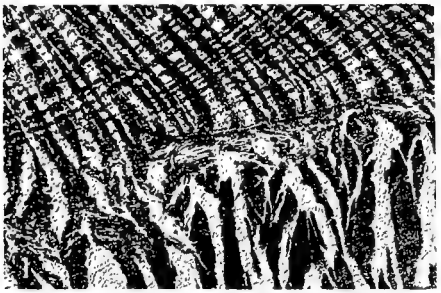
FIG. 3. Radial section of the outer crossed-lamellar layer of ***Laevicardium alternatum.*** Acetate peel, × 160.

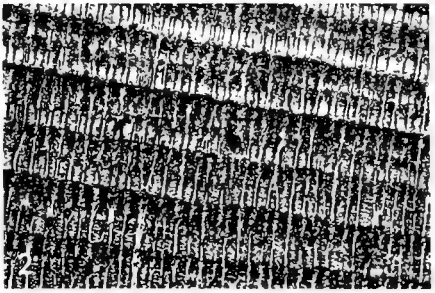
FIG. 4. Inner complex crossed-lamellar layer of ***Cerastoderma edule***; radial section. Acetate peel, × 160

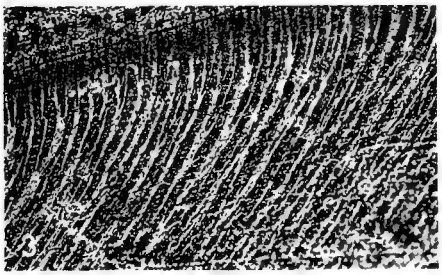
FIG. 5. Radial section of the outer crossed-lamellar layer of ***Hippopus hippopus*** showing the change in orientation of first order lamels associated with strong ribbing. Acetate peel, × 40.

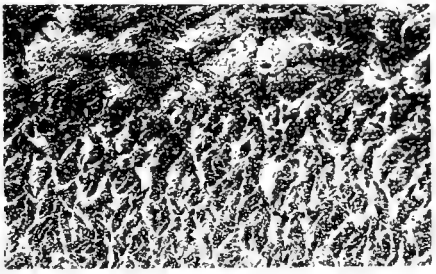
FIG. 6. Radial section of the outer crossed-lamellar layer of ***Tridacna squamosa*** showing several first order lamels with constituent lath-like, second order lamels inclined in opposing directions in adjacent first order lamels. Acetate peel, × 160.

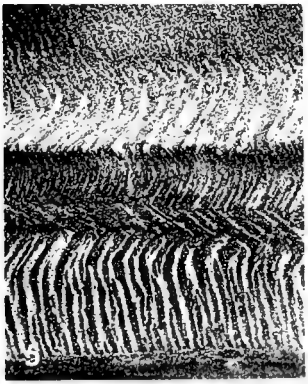
FIGS 7 & 8. Radial sections of ***Hippopus hippopus***, inner layer. Fig. 7 is a scanning electron-micrograph (× 1,200) of the structure which in the optical micrograph (Fig. 8, × 160) appears homogeneous and banded. The banding consists of sheets of aragonite needles arranged with their long axes normal to the plane of the sheet.

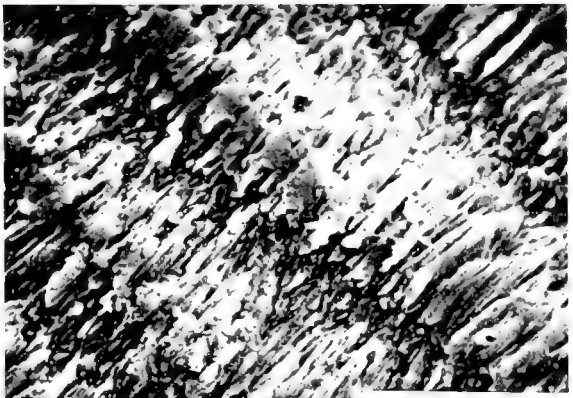


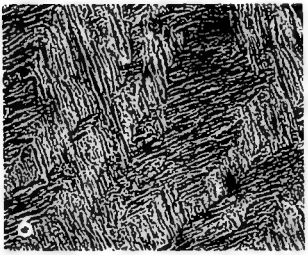












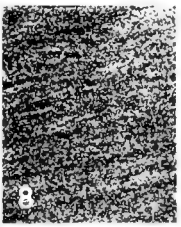


PLATE 4

FIG. 1. Radial section of ***Mactronella exoleta*** showing boundary between outer crossed-lamellar and inner complex crossed-lamellar layers. Acetate peel, × 40.

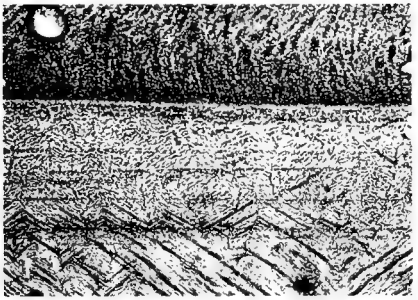
FIG. 2. Outer crossed-lamellar layer of ***Mactra producta*** showing the very thin lamels characteristic of this family. Acetate peel, × 80.

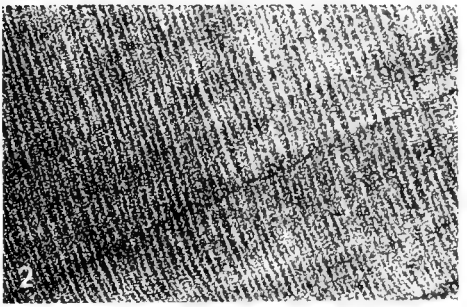
FIG. 3. Radial section of the inner layer of ***Ensis siliqua*** showing how this layer is built up of sheets of prisms, alternating with sheets of complex crossed-lamellar structure. Scanning electron-micrograph × 2,000.

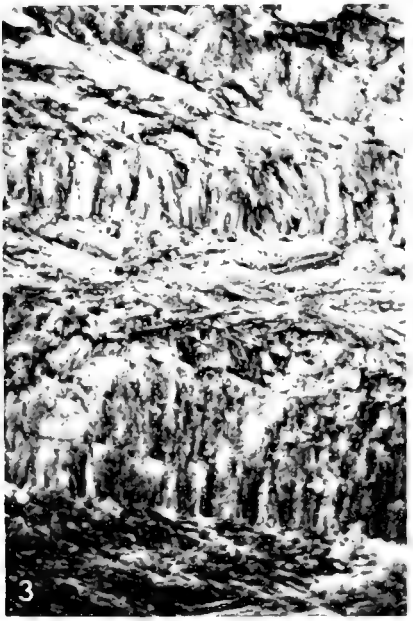
FIG. 4. Polished, etched, radial section of the middle crossed-lamellar layer of ***Hecuba scortum***. Scanning electron-micrograph, × 2,000.

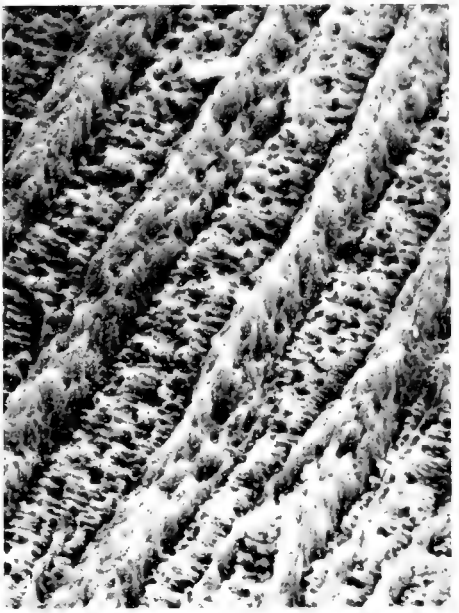
FIG. 5. Radial section of the junction between the outer composite prismatic and the middle crossed-lamellar layers of ***Donax faba***. Scanning electron-micrograph, × 1,600.

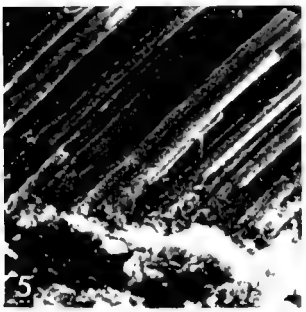
FIG. 6. Radial section of the composite prismatic layer of ***Donax faba*** showing the long, lath-shaped units of this structure as found in this family. Scanning electron-micrograph, × 2,000.











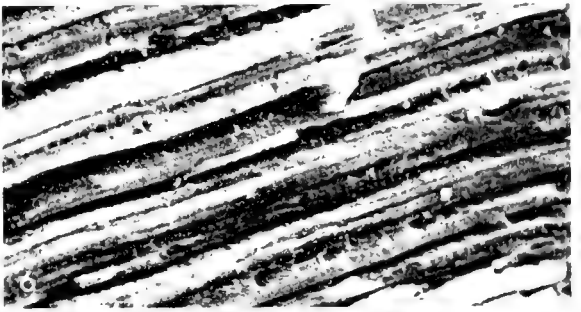


PLATE 5

FIG. 1. Polished, etched, section of the inner prismatic layer (myostracal prisms) of ***Semele tortuosa.*** Scanning electron-micrograph, × 600.

FIG. 2. As Fig. 1; showing middle crossed-lamellar layer and the inner prismatic layer separated by a thin sheet of myostracal prisms of the pallial myostracum. Scanning electron-micrograph, × 2,000.

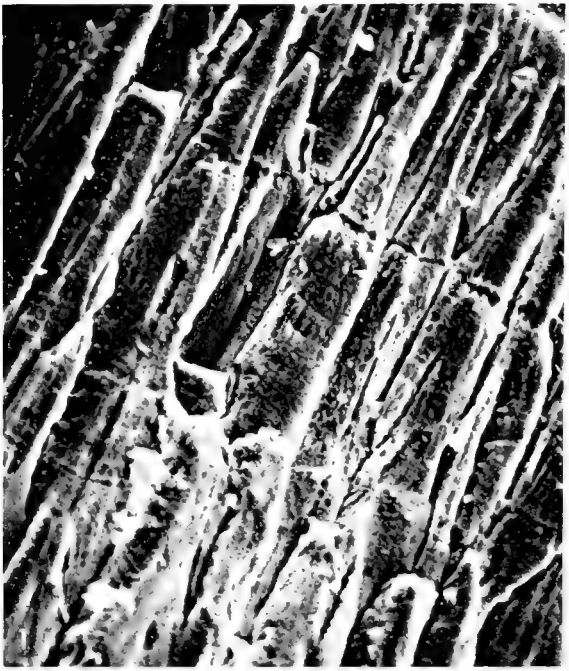
FIG. 3. Radial section of the middle crossed-lamellar layer of ***Solenotellina radiata*** showing very narrow first order lamels. Acetate peel, × 80.

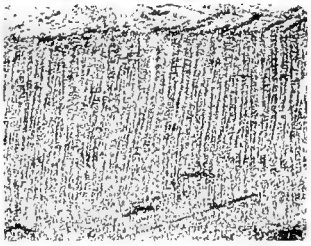
FIG. 4. Radial section of ***Semele tortuosa*** with outer composite prismatic layer (top right), middle crossed-lamellar layer and an inner layer composed of myostracal prisms. Acetate peel, × 40

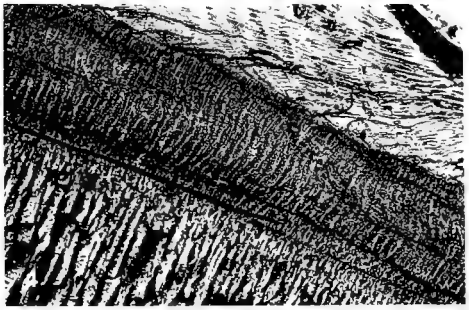
FIG. 5. Complex crossed-lamellar inner layer of ***Asaphis deflorata.*** Acetate peel, × 40.

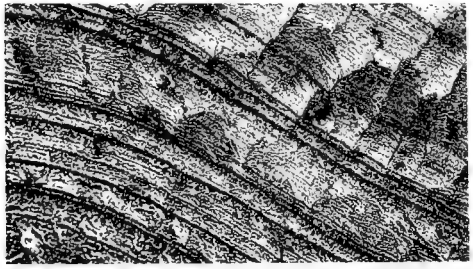
FIG. 6. Radial section of inner complex crossed-lamellar layer of ***Solenotellina radiata.*** Acetate peel, × 80

FIG. 7. Radial section of the inner homogeneous layer of ***Tellina radiata*** showing lamellate character produced by organic sheets. Acetate peel, × 80.

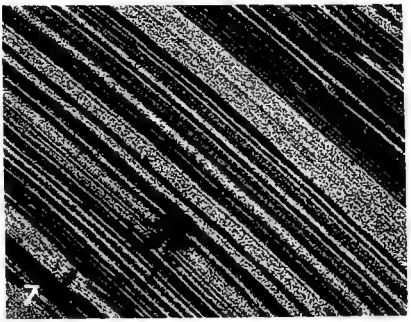








6



7

PLATE 6

FIG. 1. Radial section of the outer crossed-lamellar layer of ***Glossus humanus***; pallial myostracum at bottom left. Acetate peel, × 80.

FIG. 2. Radial section of the inner complex crossed-lamellar of ***Polymesoda anomalata***. Acetate peel, × 80.

FIG. 3. Polished and etched radial section of the outer crossed-lamellar layer of ***Dreissena polymorpha*** showing five adjacent lamellae. Scanning electron-micrograph, × 2,400.

FIG. 4. Radial section (polished and etched) of the outer crossed-lamellar layer of ***Sphaerium lacustris***. Scanning electron-micrograph, × 2,400.

FIG. 5. Inner surface of the inner homogeneous layer of ***Gaimardia trapezia*** showing a general alignment of granules towards the shell margin (top right). Scanning electron-micrograph, × 3,000.

FIG. 6. Fractured section of the inner homogeneous layer of ***Gaimardia trapezia***. Scanning electron-micrograph, × 800.

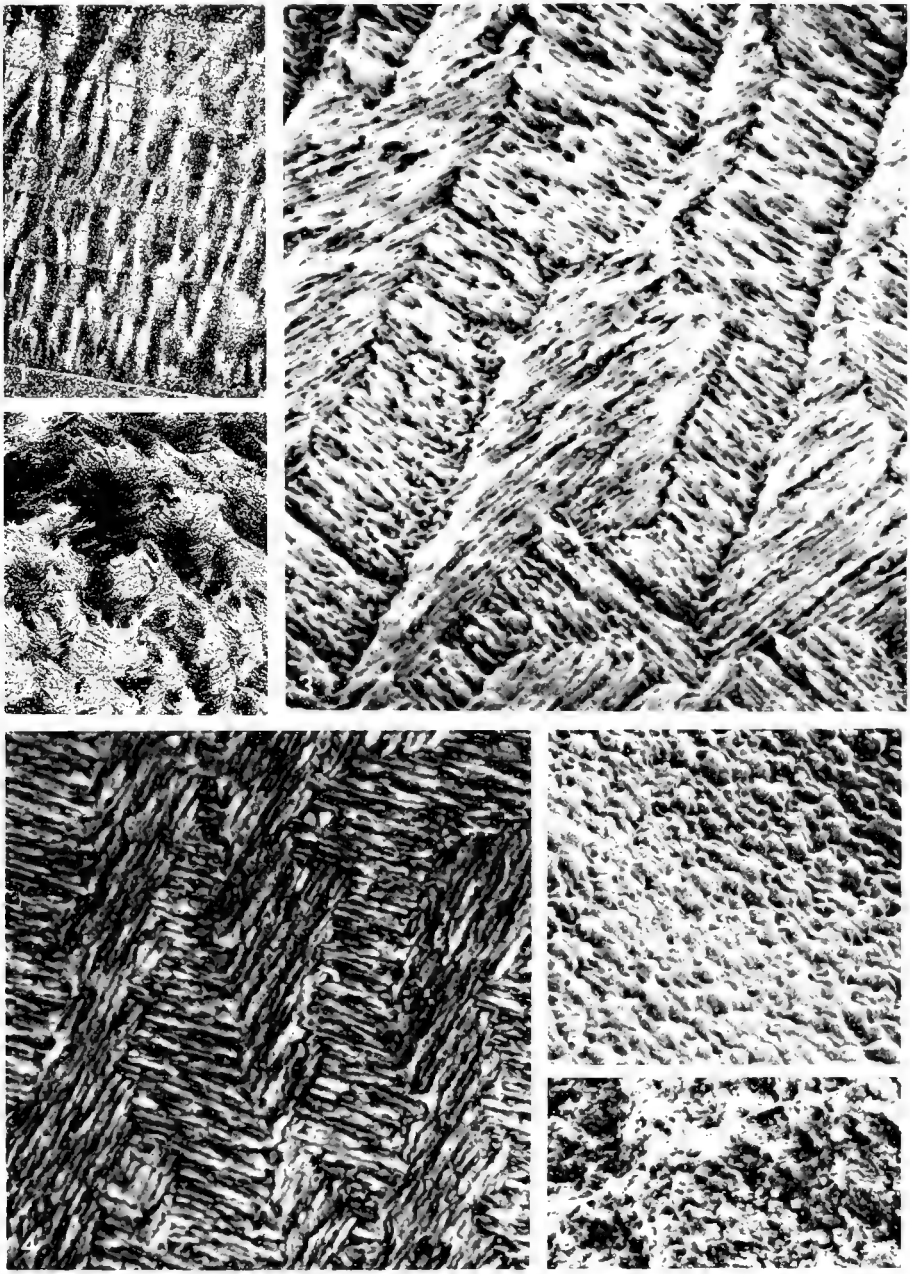


PLATE 7

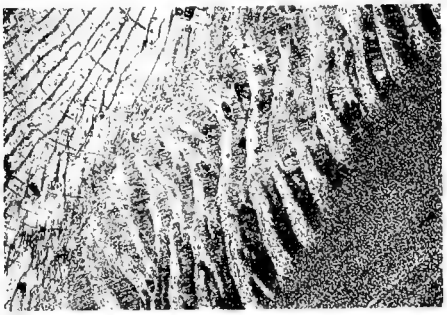
FIG. 1. Radial section of ***Venus striatula*** showing the outer composite prismatic layer (top left) and the middle crossed-lamellar layer which grades into homogeneous structure inwards (bottom right). Acetate peel, · 80.

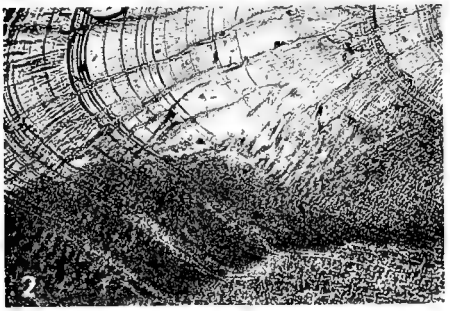
FIG. 2. Radial section of ***Venus striatula*** showing the outer composite prismatic layer (top) and the middle homogeneous layer. Acetate peel, · 80.

FIG. 3. Concentric, polished, etched, section through the outer composite prismatic layer of ***Mercenaria mercenaria*** showing the large prism units made up of small crystallites. Scanning electron micrograph, · 2,400.

FIG. 4. Radial section (polished, etched) of the outer composite prismatic layer of ***Tivela hians*** showing first order units made up of smaller crystallites in a feathery arrangement. Scanning electron micrograph, · 1,400.

FIG. 5. As Fig. 4, showing the contact between the outer composite prismatic and the middle homogeneous layers. Scanning electron micrograph, × 3,000.





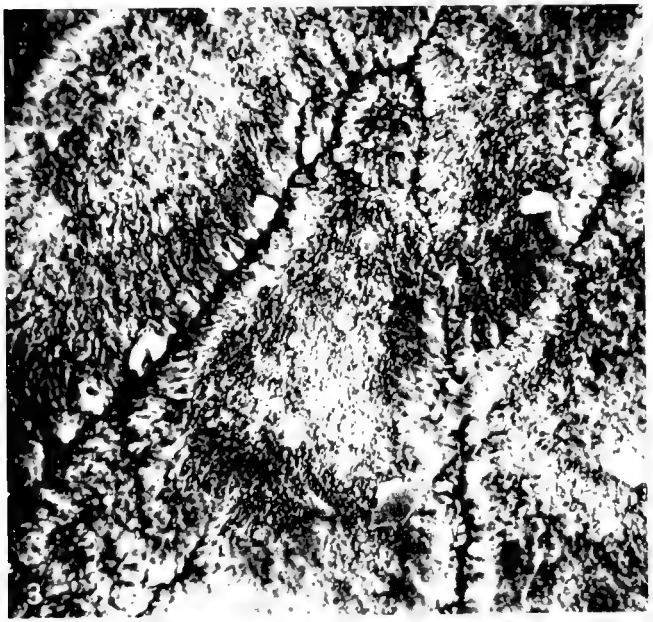


PLATE 8

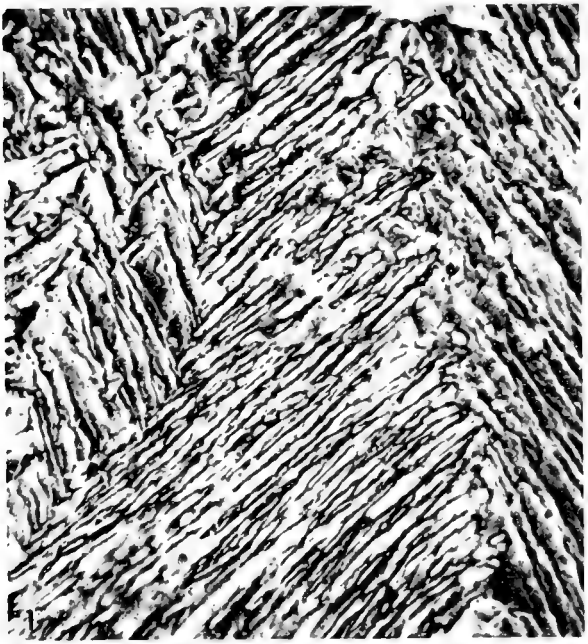
FIG. 1. Polished, etched, radial section of the crossed-lamellar middle layer of ***Mercenaria mercenaria*** showing the needle-like third order lamellae aligned in opposing directions in adjacent first order lamellae. Scanning electron-micrograph, × 2,400.

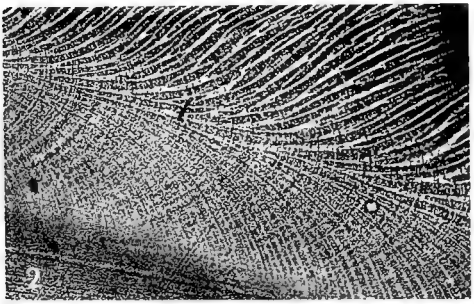
FIG. 2. Radial section of the outer crossed-lamellar layer of ***Hysteroconcha dione*** showing the crossed-lamellar structure radiating from a central axis which is aligned parallel to the outer shell surface. Note the strongly reflected growth lines. Acetate peel, × 80.

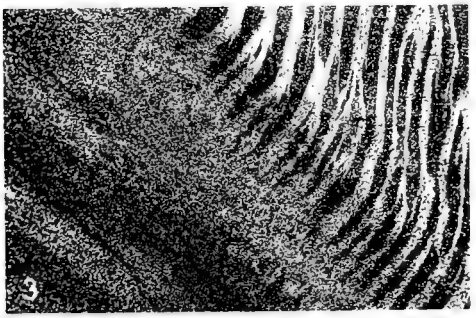
FIG. 3. Radial section of ***Gafrarium pectinatam*** showing the transitional nature of the crossed-lamellar/homogeneous boundaries in the outer shell layer. Acetate peel, × 80.

FIG. 4. Radial section of the outer crossed-lamellar layer of ***Hysteroconcha dione*** showing the arrangement of lamellae in a spine. Acetate peel, × 80.

FIG. 5. Polished, etched section of the middle 'homogeneous' layer of ***Mercenaria mercenaria*** showing the orientated nature of the crystallites. Scanning electron-micrograph, × 3,200.







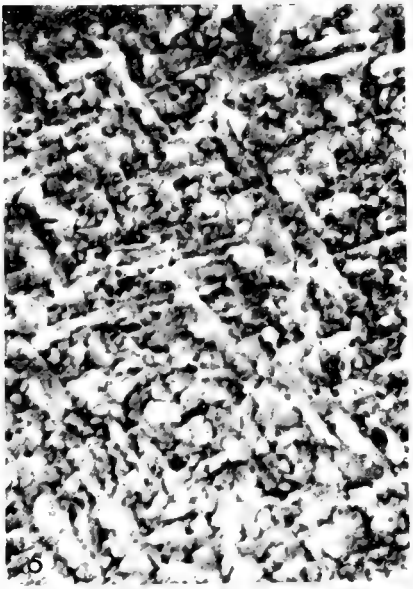


PLATE 9

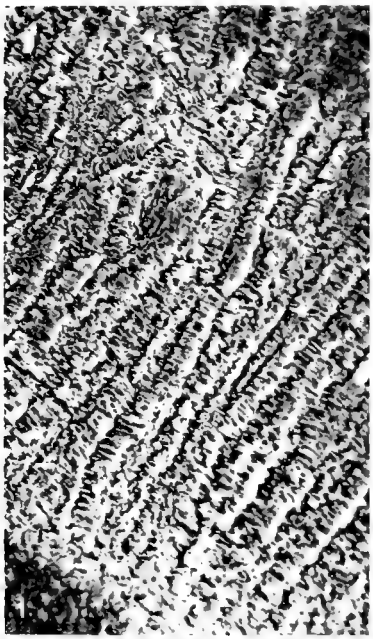
All figures are scanning electron-micrographs

FIG. 1. Polished, etched, radial section of the outer prismatic layer of ***Panopea zeylandica.*** Note the lack of a distinct interprismatic protein wall and the irregular orientation. × 650.

FIG. 2. As Fig. 1 but a detail of an individual prism showing its construction from nearly horizontal, platy crystals. × 1,200

FIG. 3. Tangential section through a prism such as Fig. 2 showing that the prism is constituted from platy crystallites which radiate from a central axis. × 1,300.

FIG. 4. Polished, etched, radial section of the inner "homogeneous" layer of ***Panopea zeylandica*** showing that at high magnifications it is made up of very fine complex crossed-lamellar structure. × 6,500.



E

PLATE 10

All figures are scanning electron-micrographs

FIG. 1. Polished, etched, radial section of ***Zirfaea crispata*** showing the outer layer (bottom left) consisting of elongate granules and the middle crossed-lamellar layer (top right). × 500.

FIG. 2. Detail of the outer layer of ***Zirfaea crispata***; heavily etched. × 1,400.

FIG. 3. Radial section (polished and etched) of the outer crossed-lamellar layer of ***Teredo navalis*** and the sharp ridges produced from this structure. × 260.

FIG. 4. Polished, heavily etched radial section of the middle crossed-lamellar layer of ***Teredo navalis.*** × 1,400.

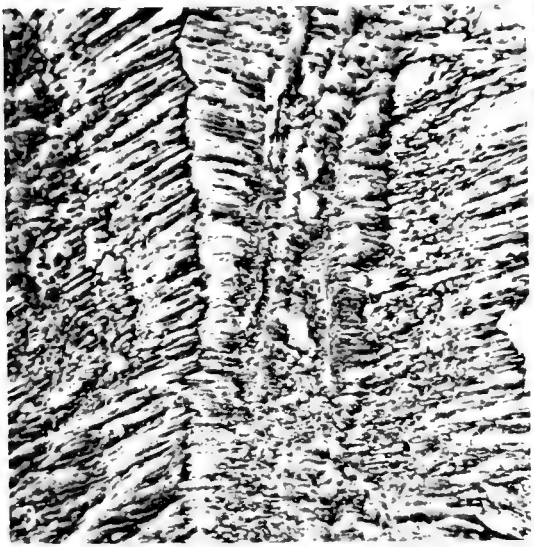


PLATE 11

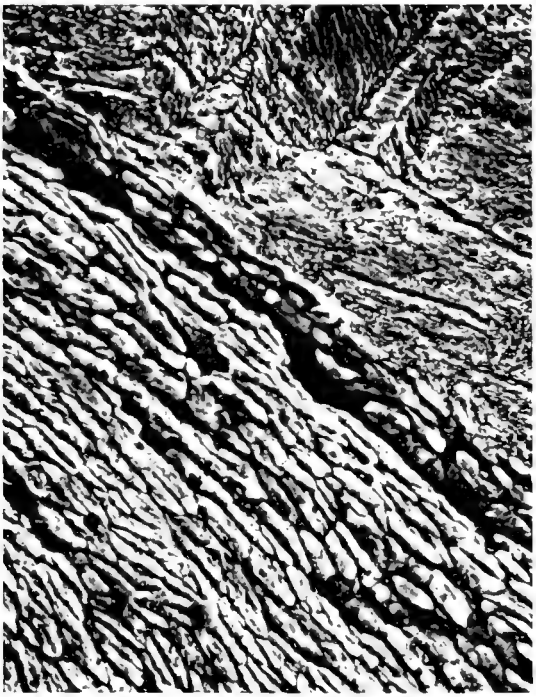
All figures are scanning electron-micrographs

FIG. 1. Radial section (polished and etched) of ***Barnea candida*** showing the outer prismatic layer (top half) and a "shoot" of the middle crossed-lamellar layer (see Text-fig. 28). The prisms are often, as shown arranged in radiating groups. × 850.

FIG. 2. As above, showing a "shoot" of the middle crossed-lamellar layer sandwiched between outer prismatic layer. × 850

FIG. 3. Detail of the outer prismatic layer of ***Pholas dactylus*** (compare with Plate 9, fig. 2 of prisms in *Panopea*). × 1,100.

FIG. 4. Polished, etched, section of the outer grey homogeneous layer of ***Mya truncata*** illustrating the formation from irregular granular crystals. × 1,200.



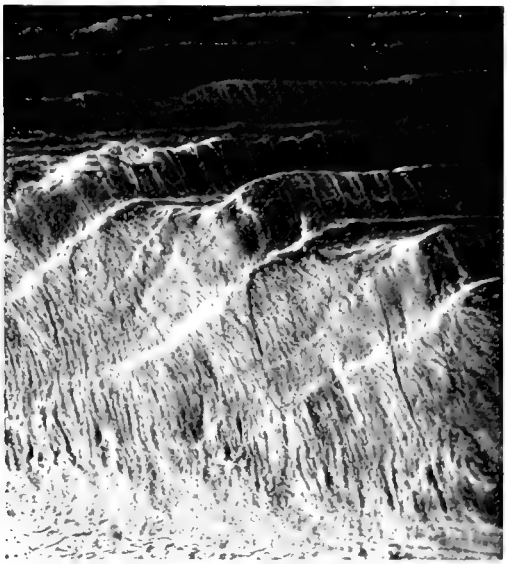


PLATE 12

All figures are scanning electron-micrographs of ***Pholadomya candida.***

FIG. 1. Fractured radial section showing the outer simple prismatic layer (top), the middle nacreous layer, pallial myostracum, and an inner layer, consisting initially of nacre and then thick sheets of myostracal prisms. × 240.

FIG. 2. Detail of the inner layer showing the sheets of myostracal prisms separated by very thin sheets of nacre (interior of shell towards top of picture). × 600.

FIG. 3. Inner nacreous layer showing sheets of nacre crystals by a sheet of myostracal prisms. × 2,400.

FIG. 4. Middle nacreous layer, compare the short bent crystals with the step-like alignment with the more regular flat sheets of larger crystals of the nacre of the inner layer in Fig. 3. × 2,400.

1

2

3

4

PLATE 13

All figures on this plate are scanning electron-micrographs

FIG. 1. ***Thracia phaseolina,*** inner surface of the outer shell layer showing individual spherulites separated by periostracum. × 1,100.

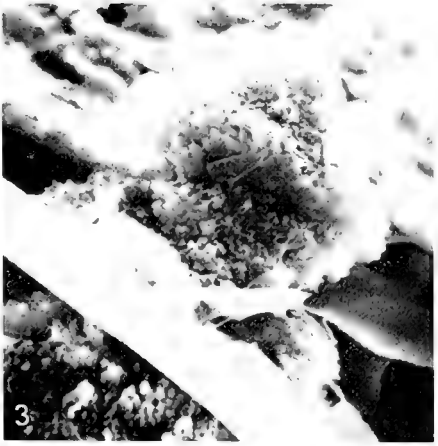
FIG. 2. Fractured section of the outer layer of ***Thracia phaseolina*** showing growing spherulites separated by sheets of periostracum. Inner shell surface to top right corner. × 800

FIG. 3. As Fig. 2 but showing detail of growing spherulite on the inner shell surface. × 3,200.

FIG. 4. Outer shell surface of ***Thracia phaseolina*** showing spherulites projecting through the periostracum. × 260.

FIG. 5. Polished, etched, radial section of the outer prismatic layer of ***Euciroa eburnea*** showing how the prisms are made up of radiating needle-like crystallites. Note the lack of sharp boundaries between prisms. × 625

1


3

4

2

5

PLATE 14

All figures are scanning electron-micrographs

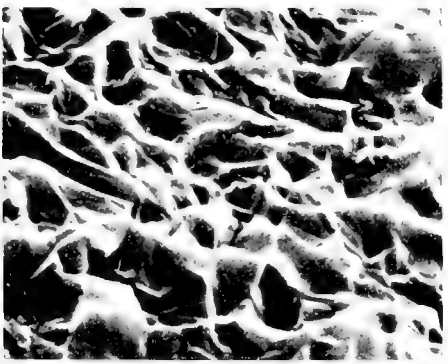
FIG. 1. Spines on the outer shell surface of ***Euciroa eburnea.*** × 220.

FIG. 2. Fractured section of the outer layer of ***Poromya granulata*** showing a section through a surface granule. × 1,100

FIG. 3. Inner shell surface of the inner homogeneous layer of ***Cuspidaria cuspidata.*** × 6,600

FIG. 4. Fractured section of the outer homogeneous layer and middle nacreous layer of ***Poromya granulata.*** × 1,100.

FIG. 5. Fractured section of ***Cuspidaria cuspidaria*** showing the outer homogeneous layer (bottom) and the inner layer resembling complex crossed-lamellar layer separated by a prismatic pallial myostracum. × 800.



4

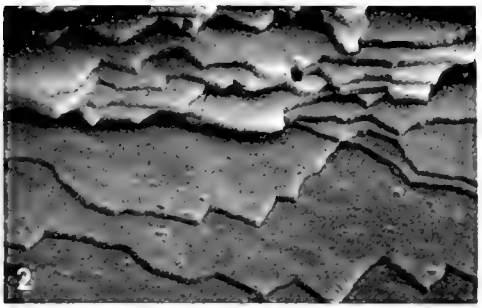
5

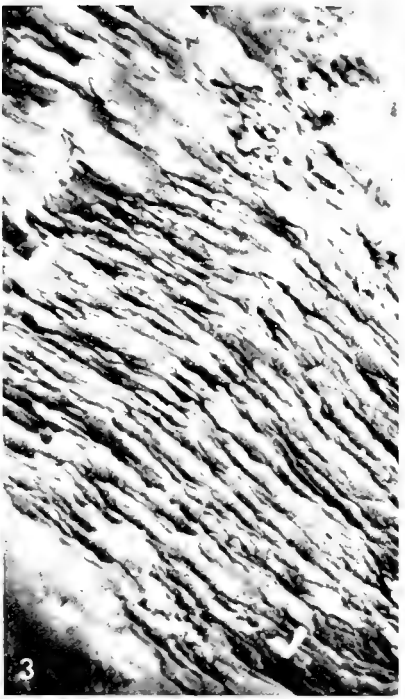
PLATE 15

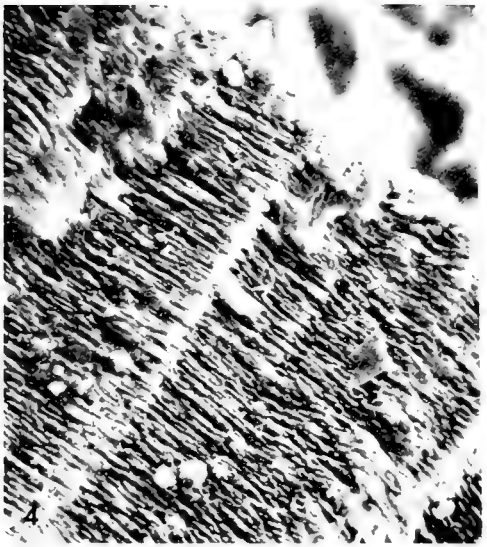
All figures are scanning electron-micrographs of ***Penicillus*** sp.

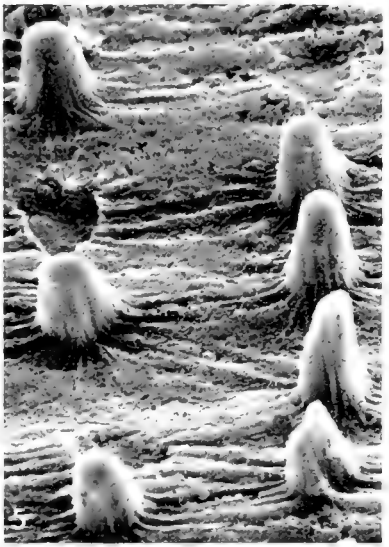
FIG. 1 Inner surface of nacreous layer. × 2,300.
FIG. 2 Fractured section of nacreous layer of valves showing sheet nacre. × 2,400.
FIG. 3 Fractured section of the tube showing the flat platy crystallites. × 2,400.
FIG. 4 As Fig. 3 but showing the stacks of platy crystallites. × 1,200.
FIG. 5. Surface granules, covered by periostracum on the outside of the true valves. The granules are arranged in rows which radiate from the umbo. × 1,300.

1


2


3


4


5

A LIST OF SUPPLEMENTS TO THE ZOOLOGICAL SERIES OF THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY)

1. KAY, E. ALISON. Marine Molluscs in the Cuming Collection British Museum (Natural History) described by William Harper Pease. Pp. 96; 14 Plates. 1965. (Out of Print.) £3.75.
2. WHITEHEAD, P. J. P. The Clupeoid Fishes described by Lacepede, Cuvier and Valenciennes. Pp. 180; 11 Plates, 15 Text-figures. 1967. £4.
3. TAYLOR, J. D., KENNEDY, W. J. & HALL, A. The Shell Structure and Mineralogy of the Bivalvia. Introduction. Nuculacea-Trigonacea. Pp. 125; 29 Plates, 77 Text-figures. 1969. £4.50.
4. HAYNES, J. R. Cardigan Bay recent Foraminifera (Cruises of the R.V. *Antur*) 1962–1964. £10.80.

Printed in England by Staples Printers Limited at their Kettering, Northants, establishment

The page numbers of the principal references and the new taxonomic names are printed in **bold** type.

Abramis 48
abyssinica, Genetta . . . 240, 247
abyssinicus, Arvicanthis niloticus . **229**–230
Acanthocardia . Tab. 6 (opp. p. 263), Pl. 3
Acomys . 219, 220, 222, 228–229, 246, 248
aculeata, Acanthocardia Tab. 6 (opp. p. 263)
aculeata, Cardita . . Tab. 4 (opp. p. 260)
acuminata, Parapholas . Tab. 19 (opp. p. 282)
acuminatus, Rhinolophus . . **185**, 194
acuminatus audax, Rhinolophus . . 185
acuminatus sumatranus, Rhinolophus . 185
acuta, Dussumieria 80
adversus, Myotis 188, 194
adversus carimatae, Myotis . . . 188
adversus moluccarum, Myotis . . 188
aeruginosus, Lithobius . . 114, 117, **133**–134
aestuarius, Gilchristella . . 65, 68, 69
aethiopicus, Paraechinus . . . 246
aethiopicus, Phacochoerus . 216, 221, 222, **243**
aethiops, Cercopithecus . .220, 221, **225**
afer, Orycteropus . . . 217, **242**
afer, Papyrocranus . . 3, 5, 7, **18**–20, 21
affinis, Carditamera . Tab. 4 (opp. p. 260)
affinis, Pitar . . Tab. 15 (opp. p. 270)
affinis macrurus, Rhinolophus . . **182**
africana, Dreissena . . 268, Tab. 12
africana, Ilisha 77
africanus, Equus 246
agilis, Lithobius **113**, 129, 143
agilis pannonicus, Lithobius . . . 113
Agripoma . . . Tab. 15 (opp. p. 270)
alata, Venus . . Tab. 15 (opp. p. 270)
albella, Sardinella 63
albicauda, Ichneumia . . .219, 221, **240**
albida, Cleidothaerus Tab. 20 (opp. p. 282), 283
albida, Pandora . Tab. 20 (opp. p. 282), 283
albipes, Praomys . . . 221, **234**, 247, 248
albipinnis, Taphozous longimanus . . 182
albocaudata, Stenocephalemys . . 247
Albula 8, 10, 44
Alcelaphus 216, 244, 245
alexandrinus, Rattus rattus . . . **235**
Allopolybothrus 108
Alosinae 70–72
alosoides, Hiodon . . . 3, 5, 7, **9**
alpestris, Lithobius dentatus . 108, 109
alpini, Procavia habessinica . . 241, 242
alpinus, Lithobius . . . **130**, 143
alternatum, Laevicardium
Tab. 6 (opp. p. 263), Pl. 3
altitudinis, Cynopterus brachyotis . . 179
amazonica, Ilisha 77
Ambonychia 288
amethystina, Caryocorbula . . . 278
Amia 8, 10, 48
Amiantis . . . Tab. 15 (opp. p. 270)
Ammodorcas 246
amnicum, Pisidium . Tab. 14 (opp. p. 269)
amomoides, Myochama Tab. 20 (opp. p. 282)
amphibius, Hippopotamus . 219, **242**–243
amplexicaudatus, Rouseltus . . **173**, 193
amplexicaudatus amplexicaudatus, Rouseltus
173
anatina, Laternula . Tab. 20 (opp. p. 282)
angasi, Offadesma . Tab. 20 (opp. p. 282)
anguilloides, Mormyrops . 3, 6, 7, **38**–40
angulatus, Cynopterus 194
angulatus, Cynopterus brachyotis . . 175
angulatus, Cynopterus sphinx . **175**–179
annae, Dosinia . . Tab. 15 (opp. p. 270)
annectans, Myotis . . **188**–190, 193
annectans, Pipistrellus . . 188, 189, 194
annectens, Pteropus hypomelanus . . 174
Anodontostoma 81
anomala, Polymesoda
Tab. 14 (opp. p. 269), Pl. 6 [anomalata]
Anomalocardia . . . 270, Tab. 15
Anomalodesmata 282
Anomiacea . . Tab. 22 (opp. p. 284), 288
antarcticum, Cyamium 260
antillarum, Crassatella . Tab. 5 (opp. p. 261)
anubis, Papio . 219, 220, 221, 222, **225**–226
aperta, Clavagella 284
Arapaima . . . 3, 5, 7, 14–16, 20, 50, 52
Arcacea . . Tab. 22 (opp. p. 284), 288
Archaeogastropoda 291
Arcoida . . . . . 286, Fig. 33
Arctica . . . Tab. 11 (opp. p. 268)
arctica, Cuspidaria . . . 282, Tab. 21
arctica, Hiatella 279, 280
Arcticacea . 256, 268, Tab. 11 (opp. p. 268),
Tab. 22 (opp. p. 284), 289
arcuata, Pandora . Tab. 20 (opp. p. 282)
arenaria, Mya 278
argentea, Pecchiola . Tab. 21 (opp. p. 282)
argyrotaenia, Clupea 80
arkelli, Thryonomys 239
aristotelensis, Parasilurus . . . 53
Artiodactyla 242–244
Arvicanthis . 217, 229–232, 246, 247, 248
Asaphis . . Tab. 10 (opp. p. 266), Pl. 5
Ascaridida 151–170
asiaticus, Bodo 99
asperatus, Lithobius 142
asperrima, Lioconcha Tab. 15 (opp. p. 270), 274
Astartacea 289

Astarte Tab. 5 (opp. p. 261), 262, Pls 1 and 2
Astartidae 261–263
Atactodea . . . Tab. 8 (opp. p. 264)
atricauda, Clupea 80
audax, Rhinolophus acuminatus . . 185
aulacopus, Lithobius 129
auratus, Engraulis . 59, **77**–79, 82, Pl. 2
aureus, Canis . . . 217, 221, **239**
australe, Laevicardium Tab. 6 (opp. p. 263)
australis, Cardita . Tab. 4 (opp. p. 260)
australis, Gouldia . Tab. 15 (opp. p. 270)
australis, Panopea 280

baelama, Thrissina 82
Bagrus 53
baloghi, Lithobius 115
balthica, Macoma Tab. 10 (opp. p. 266), 267
bane, Petrocephalus . . 3, 6, 7, **35**, 37
Barnea 279, 281, Tab. 19 (opp. p. 282), Pl. 11
beaulieui, Scotomanes (Parascotomanes) 191
bebe, Hyperopisus . . 3, 6, 7, **40**–44
beisa, Oryx gazella . . . 222, **244**
bianalis, Spratellomorpha . . . 68
bicirrhosum, Osteoglossum . 3, 5, 7, **12**–13
bicolor, Crocidura **225**
biradiata, Solentellina . Tab. 10 (opp. p. 266)
Bivalvia . . . 253–294, Pls 1–15
blanfordi, Hesperoptenus . . **191**, 194
blanfordi, Sphaerias . . . **181**, 194
blicki, Arvicanthis 230
Bodo . . . . . 87–102, Pls 1–6
boehmi, Equus burchelli . . 216, **242**
boelama, Engraulis 82
borealis, Astarte . Tab. 5 (opp. p. 261), 263, Pl. 2
borealis, Cardita . . Tab. 4 (opp. p. 260)
borealis, Lucina . . Tab. 1 (opp. p. 256)
borneensis, Coilia 83
borneensis, Rhinolophus 183, **185**–187, 193, 194
borneensis spadix, Rhinolophus . . 187
Bothropolys 142
bottazzii, Spelaeomysis . 207, 208–209
Bovidae 243–244
brachyotis, Cynopterus . 175–179, 194
brachyotis altitudinis, Cynopterus . . 179
brachyotis angulatus, Cynopterus . . 175
brachyotis brachyotis, Cynopterus **179**–181
brachyotis hoffeti, Cynopterus . . 177
brachyotis insularum, Cynopterus . . 177
brachyotis scherzeri, Cynopterus . . 177
brachyotis titthaecheilus, Cynopterus . 175
brachysoma, Clupea 80
brachysoma, Pellona 81
brachysoma, Sardinella . . . 63, 80
brandii, Dreissena . Tab. 12 (opp. p. 268)
braziliana, Anomalocardia Tab. 15 (opp. p. 270)
breviceps, Engraulis 82
breviceps, Setipinna 82
brevis, Myadora . . Tab. 20 (opp. p. 282)
brockmani, Praomys fumatus . **234**–235
brockmani internus, Claviglis . . 236
broggi, Solecurtus . Tab. 10 (opp. p. 266)
Brooker, B. E. . . . **87**–102, Pls 1–6
brucei brucei, Heterohyrax . . **242**, 248
brucei hararensis, Heterohyrax . . 242
bucculentus, Lithobius . . . **125**–126
buchholzi, Pantodon . . 5, 7, **16**–18, 50
bulgaricus, Lithobius 140
burchelli boehmi, Equus . . 216, **242**
burmanica, Clupea 70
burneti, Tellidora . Tab. 10 (opp. p. 266)
buselaphus, Alcelaphus . . 216, 245
buselaphus swaynei, Alcelaphus . 216, **244**
buxtoni, Tragelaphus 247

cadornae, Pipistrellus . . . **191**, 193
cahirinus, Acomys . . . **228**, 229
cahirinus cineraceus, Acomys . . 229
calcaratus, Lithobius **109**–110, 114, 116, 136, 137
calcarea, Macoma . Tab. 10 (opp. p. 266)
calcarina, Tellina 266
calyculata, Cardita Tab. 4 (opp. p. 260), 261
Calyptogena . . Tab. 11 (opp. p. 268)
calva, Amia 8, 10
camelopardalis, Giraffa . . . 245
Campylomormyrus . 3, 6, 7, 33–35, 40, 49, 50
cancellata, Platydon . . 276, 277, 278
candida, Barnea
279, 281, Tab. 19 (opp. p. 282), Pl. 11
candida, Pholadomya . . . 282, Pl. 12
Canidae 239
Canis 217, 221, 239, 247
cantoris, Coilia 83
canus, Pteropus hypomelanus . . 174
capensis, Lepus . . . 226, 227, 246
capensis starcki, Lepus . . . 226
Capra 246
Cardiacea . 255, Tab. 6 (opp. p. 263), 289
Cardilia . . . Tab. 8 (opp. p. 264)
Cardita . . 260, Tab. 5 (opp. p. 261), Pl. 2
Carditacea . 255, 260–261, Tab. 4 (opp. p. 260), Tab. 22 (opp. p. 284), 289
Cardium . . . Tab. 6 (opp. p. 263)
carinaria, Strigilla . Tab. 10 (opp. p. 266)
carinatus, Lithobius . . **137**–138, 139, 143
Carnivora 239–241
Caryocorbula 278
caschive, Mormyrus . . 3, 6, 23, **28**
castaneus, Scotophilus 192
castrensis, Lioconcha Tab. 15 (opp. p. 270), 273
catharia, Agripoma . Tab. 15 (opp. p. 270)
catostoma, Petrocephalus . 3, 7, 35, 36, **37**
caudatus, Bodo, . . **87**–102, pls 1–2, 4–6
Cerastoderma . Tab. 6 (opp. p. 263) Pl. 3
Cercopithecus . . . 220, 221, 225
cerina, Gouldia . . Tab. 15 (opp. p. 270)
chabaudi, Cucullanus 154
chacunda, Anodontostoma . . . 81
chacunda, Chatoessus 81

Chama 258–259
Chamacea
255, 258–259, Tab. 22 (opp. p. 284), 289, 290
Chamalea 272
chanleri, Arvicanthis . . . 231, 232
chapra, Clupea 81
chapra, Gadusia 72, 81
chaseni, Rhinolophus . . . 183, 187, 194
Chatoessus 59, 73–74, 81
chiloensis, Pholas . Tab. 19 (opp. p. 282)
Chilopoda 103–150
chinensis, Cuspidaria . Tab. 21 (opp. p. 282)
chinensis, Cyclina . Tab. 15 (opp. p. 270)
Chione . . Tab. 15 (opp. p. 270), 272
Chioninae . . Tab. 15 (opp. p. 270), 274
Chionopsis . . . Tab. 15 (opp. p. 270)
Chirocentridae 80
Chirocentrus 80
Chironax 181, 193
chitala, Notopterus 18
Chlamydoconchacea
255, 259, Tab. 22 (opp. p. 284)
ciliatum, Cardium . Tab. 6 (opp. p. 263)
cineraceus, Acomys cahirinus . . 229
cinnamomeus, Lithobius . . **135**–136
Circa . . . . Tab. 15 (opp p. 270)
Circinae . . . Tab. 15 (opp. p. 270)
Circomphalus . . Tab. 15 (opp. p. 270)
civetta, Viverra 221, **240**
clarkei, Ammodorcas 246
Clavagellacea
256, 284, Tab. 22 (opp. p. 284), 291
Clavagella 284
Claviglis 236
Cleidothaerus 282, Tab. 20 (opp. p. 282), 283
clisea, Matronella . Tab. 8 (opp. p. 264)
Clupea . . . 58, 61–63, 70–72, 80, 81
Clupeidae 61–77, 80
Clupeinae 61–63, 80
Clupeoidea 57–85
cobbi, Neodavisia 260
Codakia . Tab. 1 (opp. p. 256), 257, Pl. 1
coelophyllus, Rhinolophus . . 183, 186
coelophyllus shameli, Rhinolophus 183, 194
Coelops 187, 194
Coilia 83
Colobus 219, 220, 221, 225
Colomys 247
columbella, Lucina Tab. 1 (opp. p. 256), 257
commersonianus, Engraulis . . . 82
commersonii, Stolephorus . . . 82
communis, Lithobius . . **110**–111, 118
concamerata, Thecalia . Tab. 4 (opp. p. 260)
condorensis, Pteropus hypomelanus . 174
Congothrissa 68
consobrina, Cyrena . Tab. 14 (opp. p. 269)
continentis, Myotis hasseltii . . 188, 194
consors, Trachycardium
Tab. 6 (opp. p. 263), Pl. 3
convexa, Thracia . . Tab. 20 (opp. p. 282)
Cooperella . . . Tab. 15 (opp. p. 270)
Cooperellidae . Tab. 15 (opp. p. 270), 275
Coralliophaga . 268, Tab. 11 (opp. p. 268)
coralliophaga, Coralliophaga
Tab. 11 (opp. p. 268)
corallina, Mactra . . Tab. 8 (opp. p. 264)
Corbett, G. B. 211–252
Corbicula . . . Tab. 14 (opp. p. 269)
Corbiculacea 256, 269, Tab. 14 (opp. p. 269)
Tab. 22 (opp. p. 284), 289
Corbis . . Tab. 1 (opp. p. 256), 257
Corbula 275, 276, 278
Corbulidae 275, 291
cordata, Corbicula . Tab. 14 (opp. p. 269)
cordiformis, Arctica . Tab. 11 (opp. p. 268)
coriaceus, Lithobius . . . **124**–125
Corica 81
corrugata, Florimetis . Tab. 10 (opp. p. 266)
corsicus, Lithobius impressus . . 108
cortius, Chatoessus 81
Costia, Ichthyobodo 98
coucha, Mastomys 235
coucha lateralis, Mastomys . . . 235
crassa, Corbula 275, 278
Crassatella . Tab. 5 (opp. p. 261), Pls 1 and 2
Crassatellacea
255, 261–263, Tab. 5 (opp. p. 261),
Tab. 22 (opp. p. 284)
Crassatellidae 261–263
Crassinella . . . Tab. 5 (opp. p. 261)
crassipes, Lithobius . . 114, 115, **131**
crassum, Laevicardium Tab. 6 (opp. p. 263)
crawshayi, Lepus 227
crenata, Venerupis . Tab. 15 (opp. p. 270)
Cricetidae 227
crispata, Zirfaea . 281, Tab. 19 (opp. p. 282)
cristata, Hystrix . . . 219, **239**, 246
cristatus, Proteles . . . **240**, 248
Crithidia 99, 100
crocea, Circa . . Tab. 15 (opp. p. 270)
crocea, Tridacna . . Tab. 7 (opp. p. 264)
Crocidura 220, 221, 222, 224–225, 246, 247, 248
Crocuta 217, 221, 241
crocuta, Crocuta 217, **241**
Cryptodonta 287
Ctenodonta 286
Cucullanus 151–170
Cultellus . . 264, Tab. 9 (opp. p. 264)
cuneiformis, Corbicula . Tab. 14 (opp. p. 269)
curtipes, Lithobius . . **113**–116, 131
curtipes turkestanicus, Lithobius . . 115
Cuspidaria . . Tab. 21 (opp. p. 282), Pl. 14
cuspidaria, Cuspidaria . . . . Pl. 14
Cuspidaridae 284
cuspidata, Cuspidaria . . . . Pl. 14
Cyamiacea . 255, 260, Tab. 22 (opp. p. 284)
Cyamium 260
Cyathomonas 98
Cyclina . . . Tab. 15 (opp. p. 270)
Cyclininae . . Tab. 15 (opp. p. 270), 274

cyclotis cyclotis, Murina . . **193**, 194
Cynopterus 175–180, 194
Cyphomyrus . . 3, 6, 7, 30–31, 50, 51
cyprinoides, Marcusenius . 3, 6, 7, 10, **31**, 32
cyprinoides, Velorita . . . 269, Tab. 14
Cyrena . . . Tab. 14 (opp. p. 269)
Cyrtodaria 279, 280

dactylus, Pholas . Tab. 19 (opp. p. 282), Pl. 11
Dasymys 221, 232
Day, Francis, collections of . . . 59–61
Dayella **59**–70
decipiens, Crassatella Tab. 5 (opp. p. 261), Pl. 1
defassa, Kobus . . . 216, 222, **243**
deflorata, Asaphis Tab. 10 (opp. p. 266), Pl. 5
deignani, Myotis 188
deliciosus, Mormyrops 7, 38
dembeensis, Pelomys 247
Dendromus 219, 236, 247
dentatus, Lithobius . . . **108**, 128
dentatus var. alpestris, Lithobius . . 108
denticulata, Petricola . Tab. 15 (opp. p. 270)
deshayesiana, Verticordia Tab. 21 (opp. p. 282)
dilatata, Crassatella . Tab. 5 (opp. p. 261)
dillwyni, Meretrix . Tab. 15 (opp. p. 270)
dimidiatus, Acomys . . 220, **229**, 248
dimidiatus mullah, Acomys . . . 222
dione, Hysteroconcha
Tab. 15 (opp. p. 270), Pl. 8
diphos, Solenotellina . Tab. 10 (opp. p. 266)
(Dipodillus), Gerbillus . . . 227–228
discorhynchus, Cyphomyrus . 3, 6, 7, **30**–31, 51
dispar, Scissulina . . Tab. 10 (opp. p. 266)
ditchela, Pellona 81
ditchoa, Pellona 81
divaricatum, Gafrarium Tab. 15 (opp. p. 270)
Divaricella . . Tab. 1 (opp. p. 256), 257
divergens, Ctena . . Tab. 1 (opp. p. 256)
docmac, Bagrus 53
Donax . Tab. 10 (opp. p. 266), 267, Pl. 4
dorab, Chirocentrus 80
Dorcatragus 246
doriana, Crocidura . . . 221, **224**
Dorosomatinae 73–74, 81
Dosinia . . Tab. 15 (opp. p. 270), 274
Dosininae . . Tab. 15 (opp. p. 270), 274
Dreissena . Tab. 12 (opp. p. 268), 269, Pl. 6
Dreissenacea
256, 268, Tab. 12, Tab. 22 (opp. p. 284), 289
duboscqui, Lithobius 133
Dussumieria 68, 80
dussumieri, Coilia 83
dussumieri, Engraulis 77, 82
dussumieri, Thryssa . . . **77**–79, 82

Eason, E. H. **103**–150
eburnea, Divaricella . Tab. 1 (opp. p. 256)
eburnea, Euciroa
Tab. 21 (opp. p. 282), Pls 13 and 14
ecaudatus, Megaerops . . . **181**, 193
echinata, Acanthocardia
Tab. 6 (opp. p. 263), Pl. 3
edax, Bodo 99
Edmondiacea 291
edule, Cerastoderma Tab. 6 (opp. p. 263), Pl. 3
effosa, Lirophora . . Tab. 15 (opp. p. 270)
Egeria . . . Tab. 10 (opp. p. 266)
Ehirava . . . 64, 65, 67, 68, 69, 81
Elephantulus 223, 246
elephas, Campylomormyrus . . 6, 7, **33**–35
ellipta, Astarte . . Tab. 5 (opp. p. 261)
elongata, Ilisha 77, 81
elongatus, Lithobius 108
elongata, Oriocrassatella . . . 263
elongata, Pellona 81
elopsoides, Dussumieria . . . 80
Elops 8, 10, 48, 50
emini, Taterillus . . . 222, **228**, 248
Engraulidae 77–79, 82
Engraulis 59, 77–79, 82
Ensis . . Tab. 9 (opp. p. 264), 265, Pl. 4
ensis, Ensis . . Tab. 9 (opp. p. 264)
epidermia, Domax . Tab. 10 (opp. p. 266)
Equidae 242
Equus 216, 242, 246
Erinaceus 246
erlangeri, Gazella soemmerringi . . 244
erlangeri, Procavia habessinica . . 241
erycina, Amiantis . Tab. 15 (opp. p. 270)
erythrocephalus, Lithobius . 109, **116**, 129, 143
erythropus leucoumbrinus, Xerus . . **227**
Escualosa 80
etruscus, Suncus . . . **223**–224, 246, 248
Euciroa
Tab. 21 (opp. p. 282), 284, Pls 13 and 14
Eucrassatella . Tab. 5 (opp. p. 261), 262
Eupolybothrus . . . 108, 111, 112, 140
exogyra, Chama 259
exoleta, Mactronella
Tab 8 (opp. p. 264), 265, Pl. 4

faba, Donax Tab. 10 (opp. p. 266), 267, Pl. 4
fagani, Lepus whytei . . . **226**–227
fasciatus, Eupolybothrus . . 111, 140
fasciculata, Crithidia 99
Felidae 241
Felis 221, 222, 241, 246
ferganensis, Lithobius **115**
festivus, Lithobius **119**
fijiensis, Lucina Tab. 1 (opp. p. 256), 257, Pl. 1
filigera, Pellona 82
Fimbria . . . Tab. 1 (opp. p. 256)
fimbriata, Clupea 80
fimbriata, Corbis . Tab. 1 (opp. p. 256), 257
fimbriata, Sardinella 63, 80
fishes, clupeoid 57–85
Fishes, Osteoglossomorph . . . **1**–55
flavescens, Crocidura . . . 224, 246

flavopunctatus, Lophuromys
217, 221, **233**, 247, 248
flesus, Platichthys 153
floridana, Cardita . . Tab. 4 (opp. p. 260)
Florimetis . . . Tab. 10 (opp. p. 266)
florium toxopei, Murina . . . 193
flounder 153
fluminea, Corbicula . Tab. 14 (opp. p. 269)
fluviatilis, Ehirava . . 64, 65, 68, 69, 81
forficatus, Lithobius
107, 120, 121, 122, 124, 125, 140
forficatus var. villosus, Lithobius . . **120**
formosus, Scleropages 7
fossor, Lithobius . . . **122**–123, 124
fragilis, Gastrana . . Tab. 10 (opp. p. 266)
Fragum . . . Tab. 6 (opp. p. 263)
frithii, Coelops **187**, 194
fulvorufula, Redunca 247
fumatus, Praomys . . 222, 246, 248
fumatus allisoni, Praomys . . . 235
fumatus brockmani, Praomys . **234**–235
furthii, Ilisha 77

Gafrarium . Tab. 15 (opp. p. 270), 273, Pl. 8
Gaimardia . . . . . 268, Pl. 6
Gaimardiacea . . 256, 268, 284, Tab. 22
gairdneri, Scotophilus kuhlii . . **191**–192
Galago 225, 246
gambianus multicolor, Heliosciurus . **227**
Gastrana . . . Tab. 10 (opp. p. 266)
Gastrochaena 277, 280
Gastrochaenacea
256, 277, 280, Tab. 22 (opp. p. 284)
Gazella . . . 216, 222, 244, 245, 246
gazella, Oryx 222
gazella beisa, Oryx . . . 222, **244**
gelada, Theropithecus . . . **226**, 247
geminorum, Pteropus hypomelanus . 174
gemma, Gemma . . Tab. 15 (opp. p. 270)
Gemma . . . Tab. 15 (opp. p. 270)
Gemminae . . Tab. 15 (opp. p. 270), 274
Genetta 221, 240, 247
genetta, Genetta **240**
Gerbillinae 227
Gerbillus 222, 227–228
gibba, Corbula 276, 278
gibbosa, Eucrassatella Tab. 5 (opp. p. 261), 262
gibbosa, Sardinella 63
Gibson, D. I. 151–170
gigantea, Gastrochaena . . 277, 280
gigas, Arapaima . . . 3, 5, 7, **14**–16, 52
Gilchristella . . . 65, 67, 68, 69
Giraffa 245
glaber, Heterocephalus . . . 246
glabrata, Atactodea . Tab. 8 (opp. p. 264)
glabratus, Lithobius . . 106, **113**, 125, 127
Gliridae 236
Glossacea
256, 269, Tab. 13, Tab. 22 (opp. p. 284), 289
Glossus . . . 269, Tab. 13, Pl. 6
Gnathonemus . . 3, 6, 7, 32–33, 40, 49, 50
godanahiai, Gudusia 70
Gonialosa 73–74, 81
goslingi, Colomys 247
Gouldia . . . Tab. 15 (opp. p. 270)
gracilitarsis, Lithobius piceus . . 124
granulatus, Lithobius **131**
granti, Gazella . . . 216, **244**, 245
granulata, Chione . Tab. 15 (opp. p. 270)
granulata, Poromya
Tab. 21 (opp. p. 282), 284, Pl. 14
Graphiurus 236, 246
Greenwood, P. H. **1**–55
gregorianus, Thryonomys . **238**–239, 248
grimmia, Sylvicapra **243**
griseifrons, Dasymys incomtus . . 232
groenlandicus, Serripes . Tab. 6 (opp. p. 263)
grossipes, Eupolybothrus . .111, 112, 119
grossipes, Lithobius . . 105, 106, **111**, 112
gryphina, Chama 258
guanocostense, Trigonocardia
Tab. 6 (opp. p. 263)
Gudusia 70–72, 81
guentheri, Madoqua **243**
guereza, Colobus . . . 219, 221, **225**
Gymnarchidae . . . 3, 4, 44–48, 49, 54
Gymnarchus
3, 6, 7, 8, 10, 23, 44–48, 49, 50, 51, 52, 53

habessinica, Procavia . . 220, **241**–242, 248
habessinica alpini, Procavia . . 241, 242
habessinica erlangeri, Procavia . . 241
habessinica scioana, Procavia . . 242
habessinicus, Lepus . . . **226**, 227
hamadryas, Papio . . . 222, **226**
hamiltonii, Engraulis 82
hamiltoni, Thryssa 82
hararensis, Heterohyrax brucei . . 242
hararensis, Madoqua phillipsi . . **243**
harringtoni, Taterillus 228
harrisoni, Thryonomys . . . 238–239
hardwoodi, Gerbillus 222
harwoodi, Gerbillus (Dipodillus) . **227**–228
hasselquisti, Mormyrus . 3, 6, 7, **28**–29
hasseltii, Dussumieria 80
hasselti, Myotis 188, 194
hasseltii contintis, Myotis . . **188**, 194
haueri, Chama 258
heathi, Scotophilus 192
heathi (?) watkinsi, Scotophilus . **192**–193
hecki, Tachyoryctes . . . **237**–238
Hecuba . Tab. 10 (opp. p. 266), 267, Pl. 4
hecuba, Donax 266
Heliosciurus 227
Hemicardia . . Tab. 6 (opp. p. 263)
hemicardia, Hemicardia Tab. 6 (opp. p. 263)
henryi, Isichthys 3, 6, 7, **37**–38
Herklotsichthys 61, 80

Herpestes 240
Hesperoptenus . . . 191, 193, 194
Heterocephalus 246
heterochrous, Cucullanus 153, 157, 159, **161**–167
Heterodonta . . . 256–282, 289
Heterohyrax 242, 248
Heterotinae 14–16
Heterotis . . . 3, 5, 7, 14, 16, 18, 50, 52
hians, Tivela
Tab. 15 (opp. p. 270), 273, 274, Pl. 7
Hiatella 279, 280
Hiatellacea
256, 277, 280, Tab. 22 (opp. p. 284), 290
Hill, J. E. 171–196
Hilsa 53, 72, 81
hindei, Crocidura 224
hindei marrensis, Crocidura . . . 224
Hiodon . . . 3, 5, 7, 9, 10, 48, 50, 51
Hiodontidae 3, 9–11
Hippopotomidae 242–243
Hippopotamus 219
Hippopus . . Tab. 7 (opp. p. 264), Pl. 3
hippopus, Hippopus Tab. 7 (opp. p. 264), Pl. 3
hoevenii, Pellona 81
hoffeti, Cynopterus brachyotis . . 177
horsfieldii, Myotis 188
hortensis, Lithobius . . . **121**–122
humanus, Glossus
269, Tab. 13 (opp. p. 269), Pl. 6
Humphreysia 284
Hyaenidae 240–241
hydropica, Corbula 278
Hyperopisus . . 3, 6, 7, 40–44, 49, 50, 51
hypomelanus, Pteropus . **174**–175, 193
hypomelanus annectens, Pteropus . . 174
hypomelanus canus, Pteropus . . 174
hypomelanus condorensis, Pteropus . 174
hypomelanus geminorum, Pteropus . 174
hypomelanus lepidus, Pteropus . . 174
Hyracoidea 241–242
Hysteroconcha . Tab. 15 (opp. p. 270), Pl. 8
Hystrix 219, 239, 246

ibex nubiana, Capra 246
ibex walie, Capra 246
Ichneumia 219, 221, 240
Ichthyobodo 98
Ictalurus 53
Ictonyx 222, 239
Ilisha 74–77, 81, 82
ilisha, Clupea 81
ilisha, Hilsa 53, 81
imberbis, Muriculus 247
imberbis, Tragelaphus **244**
imbricata, Venericardia
Tab. 4 (opp. p. 260), 261
imhausi, Lophiomys 247
immutabilis, Lithobius . . . **128**–129
impressus, Lithobius . . . 106, **108**
impressus corsicus, Lithobius . . 108
impressus impressus, Eupolybothrus (Allopolybothrus) 108
inaequivalvis, Periploma Tab. 20 (opp. p. 282)
incarnatum, Vasticardium Tab. 6 (opp. p. 263)
incomptus, Dasymys . . . 221, **232**
incomtus griseifrons, Dasymys . . 232
incrassata, Astarte
Tab. 5 (opp. p. 261), 262, Pl. 1
incrassata, Cardita . Tab. 4 (opp. p. 260)
indica, Ilisha 77, 81
indica, Pellona 81
indicus, Engraulis 82
indicus, Stolephorus 82
inerbis, Tregelaphus 222
inermis, Lithobius **118**
infinitesimus, Suncus . . . 223–224
inflata, Cyrena . . Tab. 14 (opp. p. 269)
Ingle, R. W. 197–210
Insectivora 223–225
insularum, Cynopterus brachyotis . . 177
intermedia, Circa . Tab. 15 (opp. p. 270)
internus, Claviglis brockmani . . 236
internus, Graphiurus murinus . . **236**
iostoma, Chama 258
Isichthys . . . 6, 7, 37–38, 49, 50, 51
islandica, Arctica . Tab. 11 (opp. p. 268)
Isomys 230

jacksoni, Otomys 247
japonica, Dosinia 274
jebelae, Arvicanthis 230
jedoensis, Perothaca . Tab. 15 (opp. p. 270)
Jenkinsia 68

kammalensis, Engraulis . . . 82
kammalensis, Thryssa 82
kanagurta, Clupea 81
kannume, Mormyrus . . 3, 6, 7, **23**–27, 28
kapirat, Notopterus 7, 22
kelee, Hilsa 72, 81
Kelia 259
Kennerlya . . . Tab. 20 (opp. p. 282)
kijabius, Mus 235
klunzei, Clupea 80
Kobus 216, 222, 243
Koch collection (Chilopoda: Lithobiomorpha)
103–150
kuhlii, Scotophilus . . . 192, 194
kuhlii kuhlii, Scotophilus . . . 192
kuhlii gairdneri, Scotophilus . . **191**–192

lacernatus, Arvicanthis . . **230**, 232
lacerda, Mormyrus . . . 3, 6, 7, **28**
lactuosus, Cultellus . Tab. 9 (opp. p. 264)
lacustris, Sphaerium . . . . Pl. 6
Laevicardium . Tab. 6 (opp. p. 263), Pl. 3
Laeviscutella 68

Lagomorpha 226–227
lamarckii, Meiocardia . Tab. 13 (opp. p. 269)
Lamelliconcha . . Tab. 15 (opp. p. 270)
lamellosa, Crassatella . Tab. 5 (opp. p. 261)
lamellosa, Fimbria . Tab. 1 (opp. p. 256)
laminiferum, Cyamium . . . 260
lanzae, Lithobius 110
lapidicola, Lithobius 110
lateralis, Mastomys coucha . . . 235
Laternula . . . Tab. 20 (opp. p. 282)
Leggada 234
leichardti, Scleropages . . 3, 5, 7, **13**–14
leiogaster, Clupea 80
leiogaster, Sardinella 80
Leishmania 99
Lemniscomys . . 220, 232–233, 245, 248
leo, Panthera 219, **241**
Lepidomysidae 197–210
Lepidomysis . . . 199, 201, 207
Lepidophthalmus . . . 199, 201
Lepidopidae 207
Lepidops 199, 201
lepidus, Pteropus hypomelanus . . 174
Leporidae 226–227
Leptonacea . 255, 259, Tab. 22 (opp. p. 284)
leptopus, Eupolybothrus . . 111, 112
Lepus 226–227, 246
leschenaulti, Pellona 81
leschenaulti, Roussettus . . . **173**
leschenaulti leschenaulti, Rousettus . **173**
leucoumbrinus, Xerus erythropus . . **227**
leucozonica, Mactra . Tab. 8 (opp. p. 264)
liana, Lucinisca . . Tab. 1 (opp. p. 256)
libyca, Felis silvestris 241
lile, Clupea 80
Limacea . . . Tab. 22 (opp. p. 284)
Limopsacea . . Tab. 22 (opp. p. 284)
linguafelis, Scutarcopagia Tab. 10 (opp. p. 266)
Lioconcha . Tab. 15 (opp. p. 270), 273, 274
Lirophora . . . Tab. 15 (opp. p. 270)
Lithobiomorpha 103–150
Lithobius 103–150
lithophaga, Petricola . Tab. 15 (opp. p. 270)
Litocranius 222, 244
litoralis, Eupolybothrus . . 111, 112
litoralis, Lithobius . . . 105, **140**
litterata, Tapes . Tab. 15 (opp. p. 270), 274
longibarbis, Gnathonemus . .3, 6, 7, **32**–33
longiceps, Clupea 80
longiceps, Sardinella 80
longimanus albipinnis, Taphozous . . 182
longimanus longimanus, Taphozous **182**, 193
longipes, Spelaeomysis . . . 208–209
Lophiomys 247
Lophuromys . . 217, 221, 233, 247, 248
Loripes . . . Tab. 1 (opp. p. 256)
Lorisidae 225
loscombiana, Pholadidea Tab. 19 (opp. p. 282)
lovati, Dendromus 247
Loxocardium . . Tab. 6 (opp. p. 263)
lubricus, Lithobius . . . **136**–137
lucifugus, Lithobius . . 130, 131, **136**, 143
Lucina . Tab. 1 (opp. p. 256), 257, Pl. 1
Lucinacea
253, 256–257, Tab. 1, 284, Tab. 22, 289
lucinalis, Loripes . . Tab. 1 (opp. p. 256)
Lucinisca . . . Tab. 1 (opp. p. 256)
Lucinopsis . . . Tab. 1 (opp. p. 256)
lunatula, Crassinella . Tab. 5 (opp. p. 261)
lutrella, Crocidura 224
Lycaon 239

macilentus, Lithobius . . . **129**–130
Macoma . . . . 266, Tab. 10, 267
Macrocallista . . Tab. 15 (opp. p. 270)
macrocephalus hecki, Tachyoryctes **237**–238
macrocephalus macrocephalus, Tachyoryctes
237–238, 247, 248
Macroglossus 182, 194
macrolepis, Mastomys 235
macrops, Lithobius . . . 137, 138
Macroscelididae 223
macrurus, Rhinolophus affinis . . **182**
Mactra . . Tab 7 (opp. p. 264) Pl. 4
Mactracea
256, 264, Tab. 7, 265, 284, Tab. 22, 289
Mactroderma . . Tab. 8 (opp. p. 264)
Mactronella Tab. 8 (opp. p. 264), 265, Pl. 4
maculosum, Trachycardium
Tab. 6 (opp. p. 263)
madagascariensis, Sauvagella . . 67, 69
Madoqua 243, 246
magna, Scrobicularia . Tab. 10 (opp. p. 266)
mahomet, Mus . . . 217, **233**–234
malabaricus, Dayella . . **63**–67, 69, 81
malabaricus, Engraulis . . . 82
malabaricus, Spratelloides
59, **63**–67, 81, 85, pl. 16
malabaricus, Thryssa 82
malayanus, Rhinolophus . **183**, 187, 194
Mammals (other than bats) . . 211–252
manmina, Chatoessus 81
manminna, Gonialosa . . . 73, 74, 81
Marcusenius . . 3, 6, 7, 31–32, 49, 50
marmorea, Cardita
Tab. 4 (opp. p. 260), 261, Pl. 2
marrensis, Crocidura hindei . . . 224
Martesia . . Tab. 19 (opp. p. 282)
massaicus, Lemniscomys striatus . . 233
(Mastomys), Praomys 235
mearnsi, Arvicanthis 230
Megadesmus 291
Megaerops 181, 193
Megalops 10, 48
megaloptera, Ilisha 77, 82
megaloptera, Pellona 82
megalotis, Dorcatragus . . . 246
megalotis, Otocyon **239**
Megapipistrellus 189

melanocephalus, Chironax . . **181**, 193
melanocephalus, Lithobius . .106, **126**–127
melanops, Lithobius . 113, 125, 126, 127, 128
melanura, Clupea 80
melanura, Sardinella 80
Meletta 61
Mercenaria
Tab. 15 (opp. p. 270), 274, Pls 7 and 8
mercenaria, Mercenaria
Tab. 15 (opp. p. 270), 274, Pls 7 and 8
Meretricinae . Tab. 15 (opp. p. 270), 274
Meretrix . . . Tab. 15 (opp. p. 270)
martini, Cardilia . . Tab. 8 (opp. p. 264)
Matronella . . . Tab. 8 (opp. p. 264)
maxima, Tridacna . Tab. 7 (opp. p. 264)
Meiocardia . . . Tab. 13 (opp. p. 269)
Microdillus 246
microps, Lithobius 133
minimus, Lithobius **128**
minimus sobrinus, Macroglossus . **182**, 194
minor, Rhinolophus 183
minutus, Cucullanus . . 153, **155**–161, 165
minutus, Lithobius 111, **118**
modesta, Gonialosa . . . **73**–74, 81
modestus, Chatoessus . 59, **73**–74, 81, pl. 2a
moluccensis, Clupea 80
Monoplacophora 291
Monotarsobius . . . 116, 132, 133
montanus, Lithobius . . . **112**, 119
mordax, Lithobius . . . **119**–120
Mormyridae . . . 3, 22–44, 52–53
Mormyrops . . . 3, 6, 7, 38–40, 50, 51
Mormyrus . . . 3, 6, 7, 23–29, 44, 49, 50
motius, Pellona 81
Mulina . . . Tab. 8 (opp. p. 264)
mullah, Acomys dimidiatus . . 222, 229
multicolor, Heliosciurus gambianus . **227**
multispinosa, Hysteroconcha
Tab. 15 (opp. p. 270)
Muriculus 247
Muridae 228–236
Murina 193, 194
murinus, Graphiurus . . . 236, 246
murinus ? internus, Graphiurus . . **236**
murinus saturatus, Graphiurus . . 236
Mus . . 217, 219, 233–234, 235, 247, 248
muscorum, Lithobius . . . **121**, 122
Mustelidae 239
mutabilis, Lithobius
107, 110, 111, 116, 117, 118, **134**–135
muticus, Lithobius
107, 109, 110, **116**–117, 135, 136
Mya . . . . . 278, Pl. 11
Myacea . 256, 275, 278, 284, Tab. 22, 291
Myadora . . Tab. 20 (opp. p. 282), 283
Myidae 291
Myochama . . . Tab. 20 (opp. p. 282)
Myoida . 275, Fig. 33 (opp. p. 286), 290
Myomys 234
Myotis 188–190, 193, 194
Myoxus 236
Mysidacea: Lepidomysidae . . 197–210
mystacalis, Dendromus . . 219, **236**
mystax, Engraulis 82
mystax, Thryssa 82
Mytilacea . . Tab. 22 (opp. p. 284), 288
Mytiloida . . . Fig. 33 (opp. p. 286)

nasus, Nematalosa 83
natalensis, Praomys . . . 220, 221
natalensis, Praomys (Mastomys) . . **235**
Nautilus 291
navalis, Teredo . Tab. 19 (opp. p. 282), Pl. 10
nebulosus, Ictalurus 53
necator, Ichthyobodo (Costia) . . 98
Nematalosa 83
Nematoda: Ascaridida . . . 151–170
Neodavisia 260
Neolithobius 120
nigri, Xenomystus . . 5, 7, 18, **21**, 22
nigripalpis, Lithobius . . . **140**–142
Nilopegamys 247
niloticus, Arvicanthis . 217, 230, 231, 232, 246
niloticus abyssinicus, Arvicanthis . **229**–230
niloticus, Gymnarchus . 3, 6, 7, 8, 23, **44**–48
niloticus, Heterotis . . 3, 5, 7, **14**, 50
niobe, Crocidura . . . **224**–225, 248
norvegica, Panomya, Panopea (Panamya)
279, 280
Notopteridae . . . 3, 18–22, 51–52
Notopterus 7, 18, 22
nubiana, Capra ibex 246
Nucinella 287
Nuculacea . . Tab. 22 (opp. p. 284), 287
Nuculanacea . Tab. 22 (opp. p. 284), 287
nudicornis, Lithobius 108
Nuculoida . . . Fig. 33 (opp. p. 286)

obliqua, Astarte . . Tab. 5 (opp. p. 261)
obliquum, Loxocardium Tab. 6 (opp. p. 263)
oblongum, Trapezium . Tab. 11 (opp. p. 268)
occidens, Corbicula . Tab. 14 (opp. p. 269)
occidens, Psammotea . Tab. 10 (opp. p. 266)
occidentalis, Crocidura 224
Offadesma . . . Tab. 20 (opp. p. 282)
omalii, Astarte . . Tab. 5 (opp. p. 261)
oncopelti, Crithidia 100
Opisthopterus 82
Oreotragus 219, 222, 243, 248
oreotragus, Oreotragus . . 219, 222, **243**, 248
Oriocrassatella 263
orobinus, Claviglis 236
orobinus, Myoxus 236
Orycteropus 217, 221, 242
Oryx 222, 244
Osteoglossidae 3, 12–16
Osteoglossinae 12–14
Osteoglossomorpha **1**–55
Osteoglossum . 3, 5, 7, 12–13, 16, 17, 48, 50

Ostreacea . . . Tab. 22 (opp. p. 284)
Otocyon 239
Otomys 217, 247
ourebi, Ourebia 220, **243**
Ourebia 220, 243
ovata, Gastrochaena . . . 277, 280
oweni, Scientilli 259

Palaeobeterodonta 289
Palaeotaxodonta 287
palatam, Quidnipagas . Tab. 10 (opp. p. 266)
pallida, Mulina . . Tab. 8 (opp. p. 264)
Pandora . . Tab. 20 (opp. p. 282), 283
Pandoracea
256, 282, Tab. 19, Tab. 22 (opp. p. 284), 291
Pangasius 154
pangasius, Pangasius 154
pannonicus, Lithobius agilis. . . 113
Panomya 277, 279, 280
Panopea . . . 277, 279, 280, Pl. 9
Panopea (Panomya) . . 280, 284, 290
Panthera 219, 241
Pantodon . . . 3, 5, 7, 16–18, 48, 50
Pantodontidae 3, 16–18
Paphia . . Tab. 15 (opp. p. 270), 274
paphia, Chione . . Tab. 15 (opp. p. 270)
Papio . . . 219, 220, 221, 222, 225–226
Papyridea . . . Tab. 6 (opp. p. 263)
Papyrocranus . . 3, 5, 7, 18–20, 21, 22
Paraechinus 246
Parapholas . . . Tab. 19 (opp. p. 282)
Parascotomanes, Scotomanes . . 191
Parasilurus 53
pardus, Panthera 219
parisiensis, Lithobius **121**
parkinsoni, Acanthocardia Tab. 6 (opp. p. 263)
Parvicardium . . Tab. 6 (opp. p. 263)
pasha, Leggada 234
pasha, Mus . . . 219, **234**, 248
paytensis, Lamelliconcha Tab. 15 (opp. p. 270)
Pecchiola . . . Tab. 21 (opp. p. 282)
Pectinacea . . . Tab. 22 (opp. p. 284)
Pectinator 246
pectinatum, Gafrarium
Tab. 15 (opp. p. 270), Pl. 8
peeli, Microdillus 246
pelidnus, Lithobius . 107, 110, 117, 135, 136
pelliceus, Arvicanthis 230
Pellona 59, 74–77, 81, 82
Pellonulinae 63–70, 81
pellucida, Chama 258, 259
Pelomys 247
Penicillus . . . . 284, 285, Pl. 15
peregrinus, Lithobius 124
Periglypta . . Tab. 15 (opp. p. 270), 273
Periploma . . . Tab. 20 (opp. p. 282)
Perissodactyla 242
Peristedion 48
Perothaca . . . Tab. 15 (opp. p. 270)
peruviana, Lirophora . Tab. 15 (opp. p. 270)
Petricola . . . Tab. 15 (opp. p. 270)
Petricolidae . Tab. 15 (opp. p. 270), 275
Petrocephalus . . 3, 6, 7, 35–37, 49, 50
Petromyzon 154
Phacochoerus . . 216, 219, 221, 222, 243
phasa, Setipinna 82
phaseolina, Thracia
Tab. 20 (opp. p. 282), Pl. 13
phillipsi, Madoqua 246
phillipsi, Tatera robusta . . . 228
phillipsi hararensis, Madoqua . . **243**
Pholadacea . 256, 279, Tab. 19 (opp. p. 282),
Tab. 22 (opp. p. 284)
Pholadidae 279
Pholadidea . . . Tab. 19 (opp. p. 282)
pholadiformis, Petricola Tab. 15 (opp. p. 270)
Pholadomya . . . . 282, Pl. 12
Pholadomyacea
256, 282, Tab. 22 (opp. p. 284)
Pholadomyoida . Fig. 33 (opp. p. 286), 290
Pholas . . Tab. 19 (opp. p. 282), Pl. 11
Pholadomyina 282
piceus, Lithobius . . . 122, **123**–124, 140
piceus gracilitarsis, Lithobius . . 124
piceus piceus, Lithobius . . . 124
piceus verhoeffi, Lithobius . . . 124
pictus, Lycaon 239
pila, Lucina . 256, Tab. 1 (opp. p. 256)
Pinnacea . . . Tab. 22 (opp. p. 284)
Pipistrellus 188, 191, 193, 194
Pisidium . . . Tab. 14 (opp. p. 269)
Pitar . . . . Tab. 15 (opp. p.270)
Pitarinae . . Tab. 15 (opp. p. 270), 274
plana, Arctica . . Tab. 11 (opp. p. 268)
planeri, Petromyzon 154
planicostata, Venericor Tab. 4 (opp. p. 260)
Platichthys 153
Platydon 276, 277, 278
plicata, Circomphalus . Tab. 15 (opp. p. 270)
plicata plicata, Tadarida . . 193, 194
Polymesoda . Tab. 14 (opp. p. 269), Pl. 6
polymorpha, Dreissena
Tab. 12 (opp. p. 268), 269, Pl. 6
ponderosa, Calyptogena
Tab. 11 (opp. p. 268), 274
ponderosa, Dosinia . Tab. 15 (opp. p. 270)
ponderosa, Tivela . Tab. 15 (opp. p. 270)
porcus, Potamochoerus . . . **243**
Poromya . Tab. 21 (opp. p. 282), 284, Pl. 14
Poromyacea 256, Tab. 21, Tab. 22 (opp. p. 282),
284, Tab. 22 (opp. p. 284), 291
Poromyidae 284
Poromyoidea 284
Poropolys 142
Potamochoerus 243
Praomys 220, 221, 222, 234–235, 246, 247, 248
Primates 225–226
primula, Myotis . . . 189, 190, 194
Pristigasterinae 74–77, 81

pristigastroides, Ilisha 76, 77
Procavia . . 220, 222, 241–242, 247, 248
proconodon, Mus 234
producta, Mactra Tab. 8 (opp. p. 264), Pl. 4
Proteles 240, 248
Protozoa 87–102
Prowazekia 97
Psammotea . . Tab. 10 (opp. p. 266)
Pseudochama 258
Pteriacea . . . Tab. 22 (opp. p. 284)
Pteriomorphia 288
Pteroida . . . Fig. 33 (opp. p. 286)
Pteropus 174, 193
pubescens, Lithobius . . . **139**–140
puerpera, Periglypta 273
punctata, Codakia Tab. 1 (opp. p. 256), 257
punctatus, Herklotsichthys . . . 61, 80
purava, Engraulis 82
purava, Thryssa 82
pustula, Kelia 259
punctulatus, Lithobius . . **111**–112
pusillus, Lithobius . . 109, 110, 115
pusillifrater, Lithobius pusillus 109, 110, 118
pusillus pusillifrater, Lithobius 109, 110, 118
Pyramus 291
pyriformis, Tetrahymena 99

quadragesimalis, Coilia 83
quadrisulcata, Divaricella
Tab. 1 (opp. p. 256), 257
quexii, Astarte . . Tab. 5 (opp. p. 261)
Quidnipagas . . Tab. 10 (opp. p. 266)
quinterensis, Spelaeomysis . . 208–209

Raconda 82
radians, Pseudochama 258
radiata, Crassatella Tab. 5 (opp. p. 261), Pl. 2
radiata, Egeria . . Tab. 10 (opp. p. 266)
radiata, Psammotea . Tab. 10 (opp. p. 266)
radiata, Solenotellina . . . . . Pl. 5
radiata, Tellina . Tab. 10 (opp. p. 266), Pl. 5
Raeta . . Tab. 8 (opp. p. 264), 265
raffertyi, Arvicanthis 230
ramcarati, Coilia 83
Rattus 221, 235
rattus, Rattus 221
rattus alexandrinus, Rattus . . . **235**
Redunca 247
reptans, Arvicanthis . . . 231, 232
reticulata, Periglypta . Tab. 15 (opp. p. 270)
revoili, Elephantulus 246
reynaldi, Coilia 83
Rhinolophus . . . 182–187, 194
ringicula, Papyridea . Tab. 6 (opp. p. 263)
robinsoni, Rhinolophus 187
robusta, Tatera . . . 222, **228**, 248
Rodentia 227–239
rosea, Scientilla 259
rostrata, Cuspidaria . Tab. 21 (opp. p. 282)
Rousettus 173, 194
rubescens, Arvicanthis 230
rubiginosa, Genetta 240
rufescens, Elephantulus . . **223**, 246
russellii, Engraulis 82
russeliana, Raconda 82
rutilus, Xerus **227**

Salmo 48
saltans, Bodo . . . **87**–102, Pls 1–6
samharensis, Mus 235
sanguineus, Herpestes **240**
Sardinella 61, 80
saturatus, Arvicanthis 230
saturatus, Graphiurus murinus . . 236
saurus, Elops 8, 10
Sauvagella 67, 69
scherzeri, Cynopterus brachyotis . . 177
schraderi, Genetta tigrina . . . 240
Scientilli 259
scioana, Procavia habessinica . . 242
Scissulina . . . Tab. 10 (opp. p. 266)
Sciuridae 227
sclateri, Erinaceus 246
Scleropages . . . 3, 5, 7, 13–14, 50
scobinata, Scutarcopagia Tab. 10 (opp. p. 266)
scortum, Donax hecuba . . 266, 267
scortum, Hecuba
Tab. 10 (opp. p. 266), 267, Pl. 4
Scotomanes 191
Scotophilus 191–192, 194
scripta, Circa . . Tab. 15 (opp. p. 270)
scriptus, Tragelaphus . . 219, 221, **244**
Scrobicularia . . Tab. 10 (opp. p. 266)
Scutarcopagia . . Tab. 10 (opp. p. 266)
Semele . 266, Tab. 10 (opp. p. 266), Pl. 5
senegalensis, Galago . . . **225**, 246
senticosum, Trachycardium
Tab. 6 (opp. p. 263)
sericea, Crocidura . . 222, **224**, 248
sericea sericea, Crocidura 224
serratum, Laevicardium Tab. 6 (opp. p. 263)
Serripes . . . Tab. 6 (opp. p. 263)
Setipinna 82
setirostris, Engraulis 82
setirostris, Thryssa 82
serval, Felis 221, **241**
servatus, Lepidomysis 201
servatus, Lepidophthalmus . . . 201
servatus, Lepidops 201
servatus, Spelaeomysis . . 197–200, **201**–210
shameli, Rhinolophus . . **183**–185, 186
shameli, Rhinolophus coelophyllus . 194
shoana, Tatera robusta . . . 228
Sierrathrissa 68
siligorensis thaianus, Myotis . . **190**, 194
Siliqua . . . Tab. 9 (opp. p. 264)
siliqua, Cyrtodaria 280

siliqua, Ensis Tab. 9 (opp. p. 264), 265, Pl. 4
silvestris, Felis 221, 241, 246
silvestris libyca, Felis **241**
simensis, Canis 247
sindensis, Clupea . . . **61**–63, 80, Pl. 1a
sindensis, Sardinella 61, 80
sipho, Solenotellina 267
sladeni, Ilisha **74**–77, 82
sladeni, Pellona . . 59, **74**–77, 82, Pl. 2b
soborna, Corica 81
sobrinus, Macroglossus minimus . **182**, 194
soemmerringi, Gazella . . 222, **244**, 245, 246
soemmerringi erlangeri, Gazella . . . 244
solanderi, Sunetta Tab. 15 (opp. p. 270), 274
Solecurtus . . . Tab. 10 (opp. p. 266)
Solemya 287
Solemyacea . . Tab. 22 (opp. p. 284)
Solemyoida . . . Fig. 33 (opp. p. 286)
Solen . . . . Tab. 9 (opp. p. 264)
Solenacea . 256, Tab. 9 (opp. p. 264), 265, Tab. 22 (opp. p. 284)
Solenotellina Tab. 10 (opp. p. 266), 267, Pl. 5
solida, Spisula . Tab. 8 (opp. p. 264), 265
somalica, Heterohyrax 242
somalicus, Arvicanthis . **230**–231, 232, 246, 248
sordidus, Lithobius **122**, 123
Soricidae 223–225
soror, Tatera valida **228**
sowerbyi, Cardita Tab. 4 (opp. p. 260), 261, Pl. 2
spadix, Rhinolophus borneensis . . 187
spekei, Pectinator 246
Spelaeomysis 197–210
Sphaerias 181, 194
Sphaerium . . . . . Pl. 6
sphinx, Cynopterus . . . 177, 194
sphinx angulatus, Cynopterus . **175**–179
spinipes, Lithobius 119
spinosior, Bothropolys 142
Spisula . . Tab. 8 (opp. p. 264), 265
splendens, Tachyoryctes . . 236, 247
spondyliodes, Chama 259
Spratelloides . . . 59, 64, 68, 81, 85
Spratellomorpha 67, 68
squalida, Macrocallista . Tab. 15 (opp. p. 270)
sqamosa, Tridacna Tab. 7 (opp. p. 264), Pl. 3
Stolephorus 82
strangei, Humphreysia . . . 284
starcki, Lepus capensis . . . 226
stelmioides, Cucullanus . . . 154
Stenocephalemys 247
strepsiceros, Tregelaphus . . 222, **244**
striata, Astarte . . Tab. 5 (opp. p. 261)
striata, Martesia . . Tab. 19 (opp. p. 282)
striata, Myadora . Tab. 20 (opp. p. 282), 283
striatula, Chamalea 272
striatula, Venus . Tab. 15 (opp. p. 270), Pl. 7
striatus, Ictonyx 222, **239**
striatus, Lemniscomys . 220, **232**–233, 245, 248
striatus massaicus, Lemniscomys . . 233
striatus wroughtoni, Lemniscomys . 233
Strigilla . . . Tab. 10 (opp. p. 266)
strigillatus, Solecurtus . Tab. 10 (opp. p. 266)
stutchburyi, Chione . Tab. 15 (opp. p. 270)
subdiaphana, Cooperella Tab. 15 (opp. p. 270)
subimbricata, Venus . Tab. 15 (opp. p. 270)
suborbicularis, Kelia 259
subrugosa, Chione Tab. 15 (opp. p. 270), 272
sueziense, Parvicardium Tab. 6 (opp. p. 263)
suhia, Clupea 70
Suidae 243
sulcata, Astarte . Tab. 5 (opp. p. 261), Pl. 1
sulcata, Cardita . . Tab. 4 (opp. p. 260)
sulcatus, Lithobius . . **132**–133, 143
sumatranus, Rhinolophis, acuminatus . 185
Suncus 223, 246, 248
Sunetta . . Tab. 15 (opp. p. 270), 274
Sunnetinae . . Tab. 15 (opp. p. 270), 274
swaynei, Alcelaphus buselaphus . 216, **244**
swinderianus, Thryonomys . . . 239
Sylvicapra 243

Tachyoryctes . . . 236–238, 247, 248
Tadarida 193, 194
Talwar, P. K. **57**–85
Tapes . . Tab. 15 (opp. p. 270), 274
Tapetinae . . Tab. 15 (opp. p. 270), 274
Taphozous 182, 193, 194
tardoore, Opisthopterus 82
tarentolae, Leishmania 99
tartoor, Opisthopterus 82
tasmanica, Myadora . Tab. 20 (opp. p. 282)
Tatera 222, 228, 248
Taterillus 222, 228, 248
taty, Engraulis 82
taty, Setipinna 82
taylori, Tatera robusta . . . 228
telara, Engraulis 82
Tellidora . . . Tab. 10 (opp. p. 266)
Tellina . . Tab. 10 (opp. p. 266), Pl. 5
Tellinacea 256, 266, Tab. 10 (opp. p. 266), Tab. 22 (opp. p. 284), 289
temminckii, Scotophilus . . 192, 194
tenellus, Mus . . . 219, **234**, 248
Teredinidae 279
Teredo . . Tab. 19 (opp. p. 282), Pl. 10
testicularis, Isomys 230
Tetrahymena 99
textilis, Paphia . Tab. 15 (opp. p. 270), 274
thaianus, Myotis siligerensis . . **190**, 194
theobaldi theobaldi, Taphozous . **182**, 194
Theropithecus 226, 247
Thonglongya, K. 171–196
thoracata, Escualosa 80
Thracia . Tab. 20 (opp. p. 282), 293, Pl. 13
Thracidae 291
Thrissina 82
Thryonomyidae 238–239
Thryonomys . . . 220, 238–239, 248

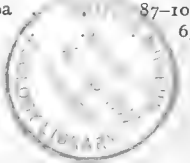
Thryssa 77–79, 82
Thyasira . . . Tab. 1 (opp. p. 256)
tickelli, Hesperoptenus . . **191**, 193
tigerina, Codakia
Tab. 1 (opp. p. 256), 257, Pl. 1
tigrina schraderi, Genetta . . . 240
tigrina, Genetta 240
titthaecheilus, Cynopterus brachyotis . 175
Tivela Tab. 15 (opp. p. 270), 273, 274, Pl. 7
toli, Clupea 81
toli, Hilsa 81
tortuosa, [illegible]nele . Tab. 10 (opp. p. 266), Pl. 5
toxopei, [illegible]ina florium . . . 193
Trachycardium . Tab. 6 (opp. p. 263), Pl. 3
Tragelaphus . . 219, 221, 222, 244, 247
transmarinus, Lithobius . . **119**, 120
transversus, Donax . Tab. 10 (opp. p. 266)
trapezia, Gaimardia . . . . Pl. 6
trapezina, Gaimardia 268
Trapezium . . . Tab. 11 (opp. p. 268)
tri, Engraulis 82
tri, Stolephorus 82
tricuspis, Lithobius . . . 125, 129
Tridacna . 264, Tab. 7 (opp. p. 264), Pl. 3
Tridacnacea 255, 264, Tab. 7 (opp. p. 264), Tab. 22 (opp. p. 284), 289
Trigonacea . . Tab. 22 (opp. p. 284), 289
trigonata, Crassatella . Tab. 5 (opp. p. 261)
Trigonocardia . . Tab. 6 (opp. p. 263)
Trigonoida . . . Fig. 33 (opp. p. 286)
trilineatus, Lithobius . . . **120**, 121
triliniata, Pandora . Tab. 20 (opp. p. 282)
truncata, Cyathomonas . . . 98
truncata, Gastrochaena . . 277, 280
truncata, Mya . . . . 278, Pl. 11
truncata, Solen . . Tab. 9 (opp. p. 264)
Trypanosomatidae . . . 87–102
Tubulidentata 242
tumidum, Gafrarium . Tab. 15 (opp. p. 270)
tunicata, Corbula 275
turkestanicus, Lithobius . . 115, 116
turkestanicus, Lithobius curtipes . . 115
typus, Otomys 217, 236

undata, Lucinopsis . Tab. 1 (opp. p. 256)
undatella, Chione 270
undulata, Raeta . Tab. 8 (opp. p. 264), 265
unedo, Fragum . . Tab. 6 (opp. p. 263)
Unionacea . 284, Tab. 22 (opp. p. 284), 289
Unionoida . . . Fig. 33 (opp. p. 286)
urinaria, Prowazekia 97

valida, Tatera 248
valida soror, Tatera **228**
validus, Lithobius 112
variegata, Cardita Tab. 4 (opp. p. 260), 261
variegata, Clupea . 59, **70**–72, 81, Pl. 1c
variegata, Gudusia . . . **70**–72, 81
variegatus, Lithobius . . .107, 134, 135
varius, Lithobius **117**
Vasticardium . . Tab. 6 (opp. p. 263)
velata, Mactroderma . Tab. 8 (opp. p. 264)
Velorita . . . Tab. 14 (opp. p. 269)
velox, Lithobius **125**
venator, Lithobius . . . **127**–128
venenosa, Clupea 61,80
venenosa, Meletta 61
Veneracea . 256, 270, Tab. 15 (opp. p. 270), Tab. 22 (opp. p. 284), 289
Venericardia . Tab. 4 (opp. p. 260), 261
Venericor . . . Tab. 4 (opp. p. 260)
Venerinae . . Tab. 15 (opp. p. 270), 273
Veneroida . 256–275, Fig. 33 (opp. p. 286), 289
Venerupis . . Tab. 15 (opp. p. 270), 274
Venus . . Tab. 15 (opp. p. 270), Pl. 7
verhoeffi Lithobius piceus . . . 124
verrucosa, Venus . . Tab. 15 (opp. p. 270)
Verticordia . . . Tab. 21 (opp. p. 282)
Verticordidae 284
vicinus, Lithobius 115
victoriae, Marcusenius . . . 3, 6, 7, **32**
villiosusulca, Thracia . Tab. 20 (opp. p. 282)
villosus, Lithobius forficatus . . . **120**
violacea, Mactra . . Tab. 8 (opp. p. 264)
virgata, Tellinella . Tab. 10 (opp. p. 266)
viriatus, Lithobius 140
vittatus, Donax . . Tab. 10 (opp. p. 266)
Viverra 221, 240
Viverridae 240
vulpes, Albula 8

walie, Capra ibex 246
walleri, Litorcanius . . . 222, **244**
watkinsi, Scotophilus heathi . . **192**–193
Whitehead, P. J. P. **57**–85
whytei, Lepus 226
whytei fageni, Lepus . . . **226**–227
wroughtoni, Lemniscomys striatus . 233
wroughtoni, Scotophilus . . . 192

Xenomystus . . 3, 5, 7, 18, 21–22, 51
Xerus 227

Yalden, D. W. 211–252

zaphiri, Arvicanthis 230
zeylandica, Panopea . . 277, 280, Pl. 9
Zirfaea . 281, Tab. 19 (opp. p. 282), Pl. 10
zoomastigophora: Protozoa . . . 87–102
zunasi, Sardinella 63